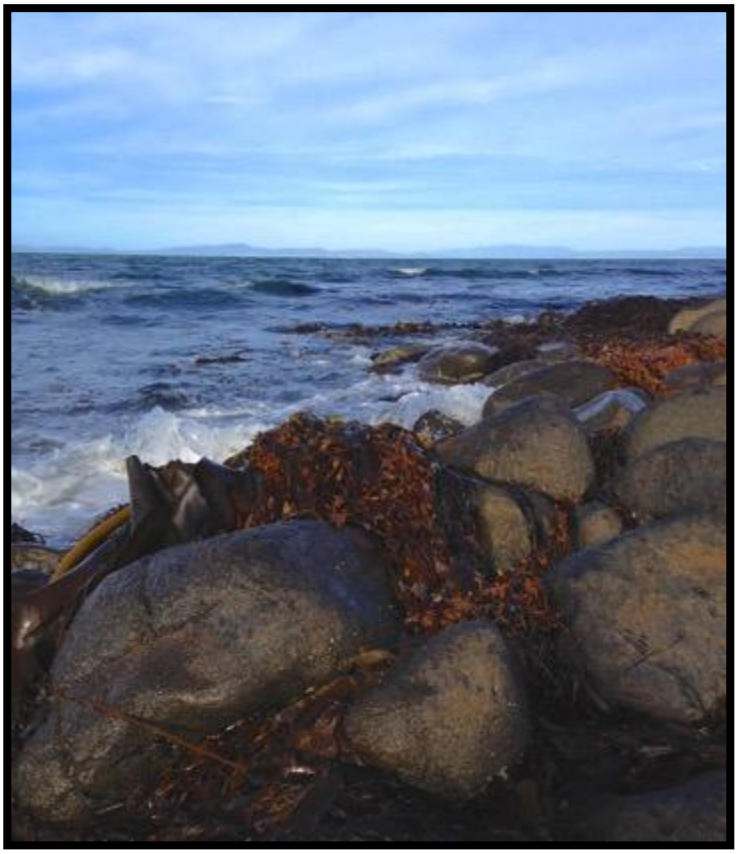
Population connectivity in marine macroalgae



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Degree of Doctor of Philosophy

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November 2015

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Chapter 2 is published as:

Durrant, H. M. S., Burridge, C. P., Kelaher, B. P., Barrett, N. S., Edgar, G. J. and Coleman, M. A. (2014). Implications of macroalgal isolation by distance for networks of Marine Protected Areas. *Conservation Biology*, 28: 438–445.

The candidate was the primary author. The Candidate conducted data analysis in collaboration with author 6. The candidate and authors 2, 3, 4, 5 and 6 contributed to the development of main ideas and approach, as well as refining the text.

Chapter 3 is published as:

Durrant H.M.S., Burridge C.P., and Gardner M.G. (2015). Isolation via next generation sequencing of microsatellites from the Tasmanian macroalgae *Lessonia corrugata* (Lessoniaceae). *Applications in Plant Sciences,* 3(7):1500042

The candidate was the primary author. Author 7 assisted with laboratory work. The candidate as well as authors 2 and 7 contributed to developing the main ideas, and approach as well as in refining the text.

Chapter 4 is in preparation:

Durrant, H.M.S., Barrett, N.S., Edgar, G.J. and Coleman, M.A., and Burridge, C.P. (in prep). The influence of habitat on population connectivity in the macroalgae *Lessonia corrugata* (Lessoniaceae)

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Chapter 5 is published as:

Durrant, H.M.S., Barrett N.S., Edgar, G.J., Coleman M.A., and Burridge C.P. (2015). Shallow phylogeographic histories of key species in a biodiversity hotspot. *Phycologia*, 54 (6): 556–565.

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Acknowledgments

I would first like to say an enormous thank you to my supervisors who have made this PhD an enjoyable learning experience, constantly taking the time to answer all of my questions and teach me at every opportunity. Your patience and support are thoroughly appreciated. Melinda Coleman who supervised me from afar and was always eager to offer assistance, despite the distance between us. Her understanding of macroalgae, locally and worldwide, has been of great benefit to the project. Neville Barrett who undertook many hours of fieldwork collecting my samples, and Graham Edgar for ARC support. Both Neville and Graham have imparted a great deal of local and scientific knowledge over the course of my project, acting as a fund of information.

A particular mention to Chris Burridge my primary supervisor. Throughout my time as his student he never ceased to amaze me in regards to the time he puts into each and every one of his students. Thank you for always having your door open, calming me down when aspects of the project failed, and for taking the time to teach me new techniques and ideas at every available opportunity. I have learnt more than I thought possible, and will always be grateful for your patience and sense of humour.

I am forever astounded and thankful for research collaboration. Sample collections would not have been possible if it were not for Liz Oh (IMAS), Rick Stuart-Smith (IMAS), Antonia Cooper (IMAS) Bryan Woods (Australian Marine Ecology), Steffan Howe (Parks Victoria), Dave Miller (DENR, SA), Alecia Belgrove (Deakin University) and Peter Unmack (University of Canberra) and Justin Hulls (IMAS). A Particular mention to Mailie Gall (Gouws *et al.*) for not only collecting samples for me, but for being a good friend and colleague.

For practical laboratory skills I would like to thank Adam Smolenski, who is an absolute asset to the UTAS genetics lab. Thank you for all the times you stayed late to teach me a new technique. No question was ever too naieve, and I can honestly say I have enjoyed the many months I spent in the laboratory. For help with everything administrative I would also like to thank the patient team we have in the School of Biological Sciences: Felicity Wilkinson, Jodi Noble, Clancy Carver, Rose Pongratz and Barry Rumbold.

For funding support I would like to thank the Holsworth Wildlife Research Endowment, for without this funding much of this research would not have been possible. Also to the Australian Research Council, University of Tasmania and the School of Biological Sciences.

Throughout my PhD I was lucky enough to have a strong network of friends to keep me sane. To those at the University of Tasmania: Gini Andersen, Nick Fountain-Jones and Anna Brüniche-Olsen, just to name a few. A particular mention to Bronwyn Fancourt, who provided coffee when it was needed most, answers to many questions, and a friendly ear when I needed to talk. Thank you also for allowing me to volunteer on your own project and get out in the field when I needed a change of scenery. Those field trips and early morning starts were a welcome change and a great experience.

To those outside of UTAS, you have been a breath of fresh air when I needed it most. Courtney Bell and Katie Caire, you've been absolutely fabulous. Joanne Steel, for our many phone calls and laughs. Dawn, Paul and Alexander Squire, for taking care of me and making me laugh. To all those mentioned here and more, I am so lucky to have found you along the way; I am surely a happier and better person for having you all in my life.

Thanks also goes to my extended family, particularly my cousin Holly for the late nights spent listening to what must have been a substantial amount of rambling on my part; it was a great distraction and release. Included in this are my inlaws (Phill, Rosemarie, Amanda and Nathan), who provided help to me in so many ways. A special mention also goes to my furry study companions, Sammy and Clancy, for their calming influence and much needed entertainment throughout my whole time at university.

To my mother Mary and father Les, if it were not for the both of you I would not have made it this far. Thank you for everything you do for me, your support and belief in me has been unwavering for as long as I can remember. It is truly a pleasure and a privilege to have you as my parents.

One of my biggest thank yous goes to my husband Brad. Even whilst coping with his wifes PhD induced mood swings, he still managed to provide a calming influence to my life. His constant support and encouragement has helped me reach the end of this road, and I am

grateful to have had him to share it with. Thank you for everything you do, I cannot wait for our next unexpected journey together.

Lastly I would like to dedicate this thesis to my grandmother, Judith, who I lost at the beginning of this journey. Your utter dedication to continual learning, in whatever form it came to you, was extraordinary. I will be forever grateful for having such a strong woman in my life, who showed me what a special gift an inquisitive mind can be. Thank you for the 24 lovely years we spent together.

Abstract

With the worldwide decline of temperate marine macroalgal populations, it is becoming important that efforts are made to reduce the impact of anthropogenic stressors faced by these communities through implementing networks of Marine Protected Areas (MPAs). The degree to which macroalgal communities will be affected by future climate change and anthropogenic disturbance will not only impact macroalgal populations directly, but the diverse suite of marine organisms they support. The aims of this thesis were to establish general dispersal capabilities of macroalage, as well as to quantify the geographic spacing of over which gene flow is maintained. Furthermore, through genetic analysis I investigated the historical and contemporary processes that have shaped the genetic structure of key southeast Australian macroalgal populations. These results will help to determine ideal configurations of MPAs intended to conserve macroalgae, as well as highlight historical and contemporary dispersal barriers that may impact population connectivity and determine the placement of marine reserves.

A meta-analysis was performed using a collection of published studies spanning a variety of macroalgal species and geographic regions (Chapter 2), to determine whether isolation by distance (IBD) relationships were generally seen amongst macroalgae. Although individual studies report IBD regression coefficients, a review such as this is lacking within the literature. A general trend of IBD was found across all studies, and was consistent across species life histories, habitat and genetic marker type. Additionally, an optimal spacing of 50–100 km between populations would facilitate a suitable level of gene flow and maintain connectivity. This chapter is published in *Conservation Biology*.

Chapter 3 is published in *Applications in Plant Sciences* and describes the development of microsatellite loci for the Tasmanian endemic macroalgae *Lessonia corrugata*. Microsatellites were identified using next generation sequencing techniques and 29 loci were screened for polymorphism; seven loci were polymorphic and optimised for future use in population genetic assessments. Samples from 14 spatially discrete populations of this species were analysed from the Derwent Estuary, Tasmania (Chapter 4). The proportion of intervening habitat types (sand, rock and open water) and marine distance, between each of these locations, was quantified and incorporated into Linear Mixed Effects models to determine their relative influence on population genetic structure.

Dispersal between populations of *L. corrugata* was limited by increases in intervening marine distance, as well as by larger proportions of open water (deeper than the euphotic zone) between sites. Proportions of intervening benthic habitat (rock/sand) also influenced genetic structure, with sand reducing gene flow.

Chapter 5 assesses the phylogeography of four key southeast Australian habitat forming macroalgal species across known biogeographic provinces. Mitochondrial and chloroplast genetic markers were used to define the phylogeographic structure of: *Ecklonia radiata*, *Macrocystis pyrifera*, *Phyllospora comosa*, and *Lessonia corrugata*. Phylogeographic variation of *E. radiata* and *L. corrugata* corresponded to historical barriers to dispersal inferred for other species. Both *M. pyrifera* and *P. comosa* lacked any phylogeographic structuring and spatial genetic variation across the entire distribution of samples. Shallow genetic variation indicates a potential recent arrival (< 3 Mya) of habitat forming macroalgae in temperate Australia. The shallow genetic variation among these species raises concerns for the future of these macroalgal populations under climate change scenarios. These results also confirmed that sampled populations of *L. corrugata* in Chapter 4 form a single deme, and therefore observed contemporary population genetic structuring cannot be attributed to historical processes. This chapter is published in *Phycologia*.

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Chapter 1

General introduction

1.1 Threats to marine ecosystems

Worldwide, marine communities are facing environmental and climatic changes, increases in anthropogenic stressors, and range expansions of highly adaptive and competitive invasive species. With the advent of the industrial revolution, atmospheric carbon dioxide levels have substantially and rapidly increased, bringing about the beginning of anthropogenic induced climate change (IPCC 2014). In a relatively short space of time humans have changed the course of Earth's climatic future, with species now facing increasing fluctuations in ocean temperatures, ocean acidification, and sea level rise. The problem is not simply that the environment is changing, but it is the rate at which these changes are occurring that is of concern.

Species dispersal capabilities play a large role in determining ecosystem diversity and population persistence in times of stress. Species capable of long distance dispersal are likely to colonise habitats away from areas impacted by anthropogenic and environmental stressors (Simpson *et al.* 2014). Species with limited capacity for dispersal or adaptation will most likely be the first to become extinct, whereas those more mobile or adaptable will have a greater chance of persisting in a changing environment (Stachowicz *et al.* 2002; Willis *et al.* 2010). Populations of the highly mobile copepod *Calanus finmarchicus,* for example, were found to shift their distributional ranges in accordance with fluctuating environmental conditions through their ability for long distance dispersal (Provan *et al.* 2009). These dispersal abilities allow *C. finmarchicus* to persist through unsuitable climatic periods and conserve populations by colonising new habitats and maintaining gene flow between existing populations. In contrast, species with reduced dispersal capabilities may have difficulty recovering after disturbance events. This was found in the scallop *Argopecten irradians concentricus*, whose population numbers declined after a significant algal bloom (Peterson and Summerson 1992). Due to limited dispersal capabilities, neighbouring populations were unable to replenish those negatively impacted, and self-recruitment was unsuccessful owing to reduced adult scallop densities.

1.2 The loss of foundation species

Although the loss or decline of any species is significant, the loss of foundation species will prove particularly detrimental (Ellison *et al.* 2005; Hobday *et al.* 2006). Macroalgae play a disproportionally important role in marine biodiversity on a global scale through their functioning as "foundation species" (Dayton 1985), supporting some of the most diverse ecosystems in the world (Mann 1973; Dayton 1985). Not only have macroalgae been found to support a larger variety of associated marine species in comparison to habitats without macroalgae (Murphy *et al.* 2000), but the removal of these habitat-forming species has the potential to reduce species abundance and taxonomic diversity in macroalgal associated communities (Bodkin 1988; Ling 2008). These macroalgal beds also act as primary producers for an array of marine organisms (Lobban and Harrison 1994), as well as providing habitat and protection from predators for a wide range of economically and ecologically important species (Tsukidate 1984; Coleman and Williams 2002). Macroalgae are also harvested for food, pharmaceutical and aquaculture industries (Smit 2004; Bixler and Porse 2011).

Macroalgal populations have been undergoing substantial range shifts and in some cases have faced major declines in range and abundance (e.g., Dayton and Tegner 1984; Zimmerman and Robertson 1985; Steneck *et al.* 2002). After catastrophic disturbance events, some macroalgae can have difficulties recovering due to a culmination of factors. For example, populations of *Macrocystis pyrifera* (L.) C.Agardh were slow to recover after their initial removal from the Californian coastline due to El Niño events in 1957-59 and 1982-83. Community assessments after the 1982-83 El Niño found that although sea urchin grazing may have hindered initial recovery, it was the anthropogenic stressors that began after the 1957-59 El Niño that had a permanent impact on macroalgal recovery, demonstrating the detrimental effects that interacting climatic and anthropogenic disturbances can have on marine ecosystems (Dayton and Tegner 1984; Glynn 1988).

1.3 Ameliorating threats to marine communities

With the accumulation of stressors facing marine ecosystems, it has become vital to protect communities and ameliorate disturbances, so as to preserve biodiversity and ecosystem

functioning. Marine Protected Areas (MPAs) represent an important tool for conserving areas of importance by restricting recreational and commercial activities in designated zones, reducing the overall stress faced by marine communities (Hoegh-Guldberg 2004; Fernandes *et al.* 2005; Jones *et al.* 2007). The spacing of MPAs, however, is a crucial aspect in their design, as this can influence the connectivity of protected populations, and contribute to the success or failure in conserving species and gene flow (Sala *et al.* 2002; Wright *et al.* 2015). Insuring connectivity between populations maintains gene flow and insures genetic variability, and can increase ecosystem resilience (Gonzalez *et al.* 1998; Palumbi 2003; Shanks *et al.* 2003; Almany *et al.* 2009). Connectivity among populations and networks of reserves can be assessed using particle dispersal models (Coleman *et al.* 2011a; Coleman *et al.* 2011b; Garavelli *et al.* 2014), however these may not represent realised patterns of species dispersal. Genetic analysis, however, allows us to directly assess the degree to which populations are connected, providing an indication of how well current MPAs are facilitating gene flow between populations (Hellberg *et al.* 2002).

Through genetic analysis we are able to gain an understanding about the historical and contemporary processes that have influenced species dispersal and population genetic structure. Genetic analyses can also provide information on how species have responded to historical environmental changes, whether they had the ability to persist through these changes and maintain genetic connectivity and variability, and how they may react to anthropogenic disturbance and future climatic changes (Ayre and Hughes 2004; Byrne 2008). This information can be crucial to designing successful MPAs and species rehabilitation programs. In a review of the phylogeography of Australian species, Byrne (2008) found that a variety of taxa were able to persist in isolated refugia through periods of historical climate change due to the availability of suitable heterogeneous habitats, highlighting the importance of protecting and maintaining a diverse variety of habitats for species to retreat to during climatic changes.

1.4 Isolation by distance

An important first step when designing well-connected MPAs is to understand the geographic scale at which species are able to disperse, to ensure reserves are spaced to allow gene flow between populations (Salm *et al.* 2006; Almany *et al.* 2009). Isolation by

distance (IBD) is a term used to describe the tendency of organisms to reproduce more frequently with individuals geographically proximate than with individuals separated by greater geographic distances (Wright 1940; Wright 1943), and is particularly informative when considering the spacing and structure of MPA networks. Essentially, the larger the distance between populations, the more genetically distinct they become. It has generally been presumed that species with relatively restricted dispersal capabilities will display greater IBD correlation coefficients than those capable of large-scale dispersal (Thiel and Haye 2006). In addition to geographic distance, environmental variables such as intervening habitat and oceanographic currents can also influence the presence and slope of any isolation by distance relationship (Wright 1943; Slatkin 1993; Palumbi 1994).

The presence of IBD is traditionally measured with a simple correlation between genetic differentiation (e.g., F_{ST}; Rousset 1997) and geographic distance among populations. A positive linear correlation indicates the presence of IBD, with the slope inversely proportional to the spatial extent of gene flow. However, advances in habitat modeling and aerial photography now make it possible for us to obtain a more ecologically informative measure of geographic distance, and allow the assessment of habitat variables that may influence the spatial scale of genetic structuring (e.g., Iampietro *et al.* 2005; Zavalas *et al.* 2014). Straight line distances are now being replaced with fine scale measures of geographic distance that follow the track of species dispersal pathways (e.g., Brennan *et al.* 2014), and we are now able to correlate F_{ST} values against other variables such as habitat continuity (Alberto *et al.* 2011; Coleman *et al.* 2011a; Coleman 2013). In addition to geographic distance and habitat, specific attributes of species life history, such as morphology and behavior can also influence the presence and slope of IBD relationships (Ian and Paul 2007; Kitanishi *et al.* 2012).

1.5 Factors influencing gene flow and IBD

1.5.1 Life history

Reproductive strategies can influence the spatial extent of gene flow, and are important to consider when designing species-specific conservation strategies (Hamrick and Godt 1996). For macroalgae, opportunities for dispersal at each life history stage can differ

considerably, (Pearson and Brawley 1996; Pearson and Serrão 2006; Serrão and Havenhand 2009). For macroalgae employing an alternation of generations life history there are three stages at which dispersal can occur. Firstly monoecious adult plants produce spores via meiosis, at which stage dispersal potential is controlled not only by the time spores remain viable within the water column before settling (hours to days), but also by the oceanographic currents and hydrological processes unique to the site of release (Santelices 1990; Reed *et al.* 1992). Once these spores settle and attach to the substrate they develop, through mitosis, into male and female gametophytes that produce gametes through mitosis, marking the second stage at which dispersal can occur. Eggs are retained on the female gametophte and release pheromones that attract sperm, which are only capable of dispersing across small distances in comparison to spores (cm; Luning and Muller 1978; Maier *et al.* 1988; Spalding *et al.* 2007). If fertilisation is successful then the resulting zygote develops into an adult plant, which while typically attached to the substrate, can become detached through storm events or herbivory. These detached plants represent the final stage for potential dispersal, with some macroalgal species capable of floating as fertile drift and remaining reproductively viable for long periods (Deysher and Norton 1981; Macaya *et al.* 2005; Muhlin *et al.* 2008). In comparison to a life history involving alternation of generations, species with simple life histories (monecious or dioecious species) do not produce spores; instead adult plants produce gametes through meiosis that are released directly into the water column, which then fertilise and grow into adults. Such species are capable of dispersal at only two stages in their life history; as gametes or zygotes and whole plants.

Regardless of the life history strategy, fertilisation hinges on whether individuals are proximate enough to allow male and female gametes to fertilise. If large patches of macroalgae are removed through storm damage or herbivory, and nearby refugia are non-existent, then species employing dioecious reproductive life histories may be slow to recover due to their inability to self-fertilise. This could inhibit the ability of dioecious species to persist at low densities or founder new populations. In contrast, macroalgae employing a monecious or alternation of generations reproductive life history are generally capable of self-fertilisation, which, although it can limit genetic variability, can also be advantageous in times of stress as it insures reproductive success (Raimondi *et al.* 2004;

Theologidis *et al.* 2014). Clonality (self-fertlisation) has been found to account for high genetic connectivity in some macroalgal populations distributed over large distances. The primary reason for this is possibly due to rafting adults using self-fertilisation as a strategy to ensure successful reproduction (Pereyra *et al.* 2013).

In addition to the variation in dispersal opportunities during reproduction, morphology can also play a large role in adult macroalgal dispersal as it has the potential to control an individual's buoyancy, thus influencing dispersal distance and IBD relationships. Gas filled bladders (vesicles) can be found on some species, which not only provide buoyancy to allow plants to remain upright in the water column and receive sunlight for photosynthesis, but also facilitate flotation and dispersal in detached adult plants (Dayton 1985). In periods of storm activity adult plants can become detached from the substrate, and have been seen drifting in large patches on the water surface, occasionally 5000 km offshore (Smith 2002). In contrast, some species of macroalgae, such as *Lessonia corrugata* Lucas, lack these flotation structures and possess heavy holdfasts through their adaptation to high impact environments like exposed rocky reefs (Koehl 1986; Tellier *et al.* 2009). In these cases, adults have limited capacity for dispersal and may display IBD relationships at shorter spatial scales than species with greater potential for adult dispersal (Coleman and Kelaher 2009; Coleman *et al.* 2011a).

1.5.2 Generality of IBD

While a general relationship of isolation by distance is evident across a wide variety of mobile and sessile marine species (Kinlan and Gaines 2003; Ayre *et al.* 2009; Durrant *et al.* 2014), it does not appear to be adequately explained by life history or behavior. Wright *et al*. (2015) investigated the prevalence of IBD across 11 species of fish and invertebrates along the South African coastline. Although there was a general trend of IBD in seven of these species, it was not a trend that could be attributed to life history (broadcast spawners, brooders and direct developers) or degree of mobility (mobile and sessile species). Results from Wright *et al*. (2015) and others (e.g., Ayre *et al.* 2009; Weersing and Toonen 2009) are beginning to suggest that life history factors do not serve as useful predictors of genetic structure and species dispersal in many marine animal species, however marine plants

remain understudied. These studies highlight the need for additional explanatory variables (e.g., habitat) to be incorporated into study designs.

1.5.3 Barriers to gene flow

Barriers to dispersal have also been found to play a significant role in influencing population genetic structure in a variety of marine taxa (e.g., Ayre *et al.* 2009; Tellier *et al.* 2011). Dispersal barriers can arise in many forms. For example, anthropogenic disturbance can result in fragmentation and inhospitable habitats that species are unable to recolonise (Coleman *et al.* 2008). In the marine environment, natural barriers can occur in the form of long stretches of sand (for obligate rocky reef species), benthic habitats deeper than the euphotic zone (for photosynthetic species), oceanographic currents, or even regions with high competition (Palumbi 1994; Hidas *et al.* 2007; Coleman and Kelaher 2009; DiBattista *et al.* 2014). The macroalga *Lessonia nigrescens*, for example, showed complete reproductive isolation owing to the influence of sandy beaches functioning as a barrier to gene flow along the Chilean coastline (Tellier *et al.* 2011). The location of these barriers, in addition to an understanding of species dispersal capabilities, facilitates the planning and implementation of successful conservation strategies such as MPAs and species translocations that aim to recover population numbers (e.g., Coleman and Kelaher 2009; Campbell *et al.* 2014).

1.6 Advances in seascape genetics

A large proportion of population genetic studies in marine and terrestrial ecosystems are now using landscape genetics to better explain genetic structure among and within populations (Manel and Holderegger 2013). Technological advances in a number of research areas have resulted in an increase in the number of studies now undertaking landscape and seascape genetic analyses. Advancements in marine habitat mapping and particle dispersal models has increased our knowledge about the marine environment and provided fine resolution data on habitat structure and potential dispersal pathways (Gallego *et al.* 2007; Ierodiaconou *et al.* 2007; Wright and Heyman 2008; Coscia *et al.* 2013). The statistical approaches capable of analysing these molecular and environmental data have also improved to the point that we are now able to develop biological meaningful

inferences about species dispersal capabilities and genetic structure. Finally, past methods of population genetic assessments typically utilised protein electrophoresis and plastid genetic markers, however with Next Generation Sequencing (NGS) technologies genetic marker development has become more accessible (Van Dijk *et al.* 2014).

1.6.1 Genetic sequencing advances

Developing genetic markers for use in population genetic studies has, in the past, been time consuming and costly, with previous population genetic studies of algae frequently using Random Amplified Polymorphic DNA (RAPD) genetic markers (Durrant *et al.* 2014), as microsatellite development was expensive and time consuming. Next generation sequencing describes a new wave of DNA sequencing technology that has developed over the last ten years (Henson *et al.* 2012). NGS has changed the way genetic research is conducted by allowing high throughput analysis of sequences at a far greater speed and lower cost than previous technology. By simultaneously sequencing mixtures of DNA, NGS technology has removed the need for previous time-consuming steps such as cloning, and colony hybridisation against a labeled probe (e.g., microsatellites sequence). These advances have meant a greater number of studies can incorporate microsatellite, single nucleotide polymorphism (SNP), and DNA barcoding data into their research (Van Dijk *et al.* 2014).

1.6.2 Seascape connectivity advances

The degree to which large-scale oceanographic currents impact population genetic structure has been investigated in a variety of marine species (Gilg and Hilbish 2003; Mitarai *et al.* 2009; White *et al.* 2010) including macroalgae (Coleman *et al.* 2011b; Coleman *et al.* 2013). In the context of widely dispersing species, these oceanographic models are readily available; however, species residing within the shallow subtidal to intertidal zone prove problematic, as oceanographic particle dispersal models tend to lose predictability when approaching the coastline (Alberto *et al.* 2011). This has meant that the incorporation of these models in seascape genetics for intertidal or nearshore species is difficult, as it relies on researchers developing fine scale hydrodynamic models for coastlines around the world (Muhlin *et al.* 2008). In Australia the online particle dispersal

model Aus-Connie (Condie *et al.* 2005; http://www.csiro.au/connie2/) has been upgraded in recent years to include fine scale models (resolution 200–500 m^2, down from 2.4–4.0 km^2) for a large proportion of the Australian coastline. Aus-Connie takes into account variables such as tidal flux, wind forcing, depth and temporal variability of environmental factors such as temperature and oceanographic current speeds, allowing investigation of the influences of hydrology on dispersal in intertidal species.

1.6.3 Advances in statistical methods applied to seascape genetics

Just as the processes underpinning landscape genetic data collection have improved, so too have the statistical approaches used to assess these data. In 1979 Mantel tests were first used to in the assessment of population genetics to test for correlations between genetic and habitat distances. These Mantel tests were originally designed to understand the temporal-spatial clustering of closely related diseases (Mantel 1967), however due to their reputed ability to accommodate non-independence of pairwise distances they were also found to be useful for landscape genetic assessments. In recent times however, Mantel tests have come under some criticism due to their high type I error rates and inflated correlation values in landscape genetic analyses (Balkenhol *et al.* 2009; Legendre and Fortin 2010). Although partial Mantel tests have also been used for landscape genetic assessments, like Mantel tests these are also found to exhibit similar levels of error (Guillot and Rousset 2013). Given the error rates and inflated correlation values associate with Mantel and partial Mantel tests, and their inability to assess multiple explanatory variables simultaneously, they are progressively being replaced by alternative approaches for landscape genetic analysis.

In a review of landscape statistical methodology, Balenhol *et al*. (2009) assessed 11 different approaches for analysis of a landscape genetic dataset. Their study was the first of its kind to test for alternative methods in the field of landscape genetics, and remains one of the most comprehensive and extensive reviews on landscape genetic analyses in the literature. From the total 11 methods tested, including traditional Mantel tests, the top three methods with both highest power and lowest type-I error rate were partial Canonical Correspondence Analysis (CCA), Multiple Regression of Distance Matrices (MRDM), and Bayesian Inference of Migration Rates (BIMR). Unlike a traditional CCA, partial CCA

tests have the ability to control for variables that are not of primary concern so as to determine the true influence of other predictor variables that are of primary interest. MRDM has the ability to analyse predictor variables simultaneously or by gradually building a suitable model using stepwise regression. Finally, in comparison to a large proportion of other landscape genetic analysis methods, BIMR uses pairwise migration rates as opposed to pairwise genetic distance as a response variable in its analysis of influential habitat variables. Using migration rates allows for directionality to be accounted for in analyses and the identification of source and sink populations (Holderegger and Gugerli 2012).

More recently, Van Strien *et al*. (2012) employed Linear Mixed Effects (LME) modelling to explain the influence of multiple habitat explanatory variables on spatial genetic variation. This method used Clarke *et al*. (2002) Maximum Likelihood Population Effects (MLPE), and R^2_β (Edwards *et al.* 2008) as a more accurate indication of model fit. The use of LME models also has advantages over MRDM in that it accommodates the non-independence of pairwise distances by including them as random factors in the analysis. Unlike traditional R^2 values, R^2_β does not increase simply because an additional predictor variable has been added to a model. In addition to the problems with using R^2 values, AIC values associated with traditional models are also inappropriate for MLPE methods, as these values can be influenced by the non-independence of predictor variables (Clarke *et al.* 2002).

1.7 Phylogeography

Although population genetic studies allow us to assess how contemporary processes and habitat variables influence spatial genetic variation, it is important to also understand the influence of historical factors on species spatial distributions and genetic structure. Without understanding the relative influences of contemporary and historical factors, landscape genetic inferences may be confounded (Dyer *et al.* 2010). This could lead to conservation managers being misinformed when deciding which environmental processes and habitat features to consider when designing species management programs.

The field of phylogeography aims to understand how historical processes have influenced the genetic structure and geographic distribution of populations. Formation of barriers for marine species, such as the emergence of landmasses, will separate populations, isolating individuals and preventing interbreeding. Even after barriers are removed, species can still exhibit the effects these barriers have had on dispersal through their genetic structuring (e.g., Waters *et al.* 2005; York *et al.* 2008; DiBattista *et al.* 2014). The utilisation of phylogenetic markers, which have slower mutation rates in comparison to markers like microsatellites, can also help us understand species colonisation/recolonisation pathways, and can provide insights into how species may respond to future environmental changes.

1.7.1 Historical processes

Pleistocene climate fluctuations are the most commonly tested historical factor that may leave legacies in contemporary genetic variation (Hewitt 2000). Climatic cooling can bring about the emergence of dispersal barriers for marine species in the form of ice sheets, which have the ability to remove species during periods of glaciation through ice scour (Fraser *et al.* 2010; Macaya and Zuccarello 2010b). Species recovery after glacial maxima not only stems from species persistence throughout glaciation, but can also come about by recolonisation from proximate glacial refugia. In these cases, species distributions have contracted to the point that populations only exist in isolated areas (Provan 2013). As temperature increases and sea ice retreats, population recovery can result from expansion of these refugial populations into areas previously uninhabitable (Hewitt 1996; Hoarau *et al.* 2007b; Maggs *et al.* 2008; Coyer *et al.* 2011).

In periods of climatic warming, resulting increases in sea level caused stretches of land to become submerged, allowing previously separated populations to reconnect. In temperate Australia, the best example of this is the submergence of the Bassian Isthmus, a land bridge that once connected Tasmania to mainland Australia (DiBattista *et al.* 2014). Although this land bridge disappeared 14,000 years ago, many species show genetic breaks corresponding to its placement (Waters 2008; Ayre *et al.* 2009). Australia's varying boundary currents are also thought to influence species dispersal and genetic structure by maintaining the separation of populations in this region, a role once played by the land

bridge barrier, causing east-west genetic differentiation between many marine species (York *et al.* 2008; DiBattista *et al.* 2014).

Although ice sheets and the emergence of land bridges can impede a species' ability to disperse, it is possible that temperature fluctuations may, in fact, have had a greater legacy on spatial genetic structure, forcing species to adjust their distributional range in accordance with their environmental tolerances. For temperate marine species, increases in sea surface temperatures usually result in a poleward distributional shifts (Hewitt 2004; Jentsch *et al.* 2007). However for those species already at their distributional limit, such as those in southeast Australia, this may not be possible (Bates *et al.* 2014b). Species unable to shift their distributional range may have undergone a reduction in abundance and genetic diversity, and possible extinction, while those with the ability to tolerate temperature fluctuations could persist (Wernberg *et al.* 2011).

Phylogeographic analysis can also provide information on historical dispersal routes and the timing of colonisation. It has long been hypothesized that several macroalgal lineages underwent a southward range expansion from the Northern Hemisphere into the Southern Hemisphere. This is shown through phylogenetic analysis, which revealed that macroalgae display greater spatial genetic structure in the Northern Hemisphere, owing to longer persistence of lineages in this region (Coyer *et al.* 2001; Shepherd and Edgar 2013). Species within the Southern Hemisphere show comparatively shallow genetic structure, consistent with recent colonisation from the Northern Hemisphere (Coyer *et al.* 2001; Fraser *et al.* 2010; Durrant *et al.* 2015a). This shallow genetic structure raises concerns for the future of macroalgae in the Southern Hemisphere, as they possess lower genetic variability, hindering adaptation. If they are unable to cope with a changing climate then macroalgal populations, and the associated marine organisms they support, risk extinction (Johnson *et al.* 2011a; Maclean and Wilson 2011).

1.8 Southeast Australian marine communities

Over the last 50 years southeast Australia has seen significant declines in some of its most important habitat forming macroalgae (Sanderson 1997; Coleman *et al.* 2008; Connell *et al.* 2008; Johnson *et al.* 2011a). The range extension of the East Australian Current has

resulted in increases in southeast Australian seawater temperatures. These temperature increases have led to population declines of the giant kelp (*Macrocystis pyrifera*) to the point that it was listed as a threated ecological community in 2012, the first time a marine ecosystem has been listed as threatened under Australian law (Department of the Environment 2015). Similar population declines in habitat-forming macroalgal species along the coast of Western Australia occurred during an extreme heatwave event in 2011, which saw ocean temperature rise 2–4°C above average. After this period of warming, subtidal habitat-forming macroalgal species showed significant reductions in abundance and range (Smale and Wernberg 2013; Wernberg *et al.* 2013), and marine communities as a whole were found to contain a higher number of tropical fish species after the warming event (Wernberg *et al.* 2013). Furthermore, urbanised coastlines along New South Wales have also seen substantial declines in the macroalga *Phyllospora comosa* (Labillardière) C.Agardh, with no current evidence for natural recolonisation of this region (Coleman *et al.* 2008).

With extensions in warm oceanographic currents, range expansions of herbivores have also occurred, such as the spiny sea urchin (*Centrostephanus rodgersii*), and introductions of invasive macroalgal species. These species pose a threat to native southeast Australian macroalgae through herbivory and competition, threatening the endemic marine communities that rely on these habitats for protection (Valentine and Johnson 2004; Johnson *et al.* 2005). The range expansion of *C. rodgersii* has resulted in the formation of urchin barrens along the east coast of Tasmania. Removal of native macroalgae impacts local species such as the Tasmanian rock lobster through the loss of the habitat provided by these macroalgal populations (Mislan and Babcock 2008). Furthermore these cleared habitats are susceptible to colonisation from non-native macroalgal species such as *Undaria pinnatifida* (Barrett *et al.* 2009).

In the face of climate change, marine reserves have the capacity to increase an ecosystems resistance to invasion by mitigating anthropogenic stressors faced by communities (Micheli *et al.* 2012; Bates *et al.* 2014a). Creating networks of marine reserves with a comprehensive understanding about the overall environmental processes that influence spatial genetic variation should allow for successful protection of marine biodiversity (Selkoe *et al.* 2008; Amaral *et al.* 2012). In southeastern Australia, the protection of

macroalgal habitats will not only benefit marine community biodiversity, but will help ensure the persistence of commercial industries that directly or indirectly rely on macroalgal populations.

1.9 Thesis aims

In this thesis I:

1. Investigate the global generality of patterns of macroalgal isolation by distance by undertaking a meta-analysis. (Chapter 2)
2. Assess the distances over which macroalgae maintain gene flow, as a guide for optimal marine reserve spacing. (Chapter 2)
3. Develop population genetic markers for the Tasmanian endemic macroalga *Lessonia corrugata*. (Chapter 3)
4. Explore the influences of habitat on the population genetic structure of *L. corrugata* within the Derwent Esuary. (Chapter 4)
5. Examine the phylogeography of southeastern Australian macroalgae and their relationship with historical processes. (Chapter 5)

1.10 Thesis structure

This thesis consists of six chapters, four of which have been written as articles for publication. Chapters 2 and 3 have been published in peer-reviewed journals, chapter 4 is currently under review and chapter 5 has been prepared for submission. For consistency, each chapter was slightly modified to fit with the formatting style of the thesis as a whole. All other content within chapters however reflects the published version of the article.

Chapter 2

Implications of macroalgal isolation by distance for networks of marine protected areas

This chapter is published as:

Durrant, H. M. S., Burridge, C. P., Kelaher, B. P., Barrett, N. S., Edgar, G. J. and Coleman, M. A. (2014). Implications of Macroalgal Isolation by Distance for Networks of Marine Protected Areas. *Conservation Biology*, **28**: 438–445. doi: 10.1111/cobi.12203

2.1 Summary

The global extent of macroalgal forests is declining, greatly affecting marine biodiversity at broad scales through the effects macroalgae have on ecosystem processes, habitat provision, and food web support. Networks of marine protected areas comprise one potential tool that may safeguard gene flow among macroalgal populations in the face of increasing population fragmentation caused by pollution, habitat modification, climate change, algal harvesting, trophic cascades, and other anthropogenic stressors. Optimal design of protected area networks requires knowledge of effective dispersal distances for a range of macroalgae. I conducted a global meta-analysis based on data in the published literature to determine the generality of relation between genetic differentiation and geographic distance among macroalgal populations. I also examined whether spatial genetic variation differed significantly with respect to higher taxon, life history, and habitat characteristics. I found clear evidence of population isolation by distance across a multitude of macroalgal species. Genetic and geographic distance were positively correlated across 49 studies; a modal distance of 50–100 km maintained $F_{ST} < 0.02$. This relation was consistent for all algal divisions, life cycles, habitats, and molecular marker classes investigated. Incorporating knowledge of the spatial scales of gene flow into the design of marine protected area networks will help moderate anthropogenic increases in population isolation and inbreeding and contribute to the resilience of macroalgal forests.

2.2 Introduction

Networks of marine protected areas (MPAs) are being established worldwide in an effort to conserve species and ecosystems that may be negatively affected by fishing and other forms of anthropogenic stress (Hoegh-Guldberg 2004; Fernandes *et al.* 2005; Jones *et al.* 2007). The central aim of establishing most networks of protected areas is to conserve marine biodiversity and ecological processes, an outcome more easily achieved via conservation of critical and important habitats, rather than directing management responses at species individually. Habitat-forming macroalgae, such as laminarian and fucalean kelps, comprise an important functional group that benefits from MPAs, mostly through indirect effects whereby predatory fish and lobster populations increase with restrictions on fishing and thus grazing invertebrates are suppressed, which allows recovery of macroalgal

forests (Babcock *et al.* 2010).

Macroalgal forests in turn support high faunal biodiversity in temperate marine waters (Mann 1973). They are foundation species (Dayton 1985) and as such stabilise habitats and facilitate colonisation of a variety of marine organisms by providing sanctuary from predators and otherwise harsher environmental conditions. Residing within these forests are many economically and ecologically important species that utilise these habitats as nursery grounds (Tsukidate 1984; Coleman and Williams 2002). Indeed, macroalgal forests are disproportionally important for the conservation of marine biodiversity due to the variety of species they support (Dayton 1985; Poloczanska *et al.* 2007; Wernberg *et al.* 2010), and the decline of macroalgal forests in temperate waters worldwide has ecosystem-level implications (Steneck *et al.* 2002; Thibaut *et al.* 2005; Wernberg *et al.* 2012). Human induced stressors, such as the harvesting of kelp and predators of grazers, bottom trawling over low-relief reef, pollution, coastal development, and climate change are some of the causes for decline of macroalgal forest (Dayton and Tegner 1984; Steneck *et al.* 2002; Coleman *et al.* 2008) and the biodiversity they support.

Conservation initiatives are increasingly designed to protect areas so that they may confer greater persistence and resilience in the face of future environmental change. These initiatives rely on the premise that decreasing anthropogenic stressors via regulations (e.g., harvesting and pollution) in MPAs will result in net reduction in the sum of threats, and fewer negative responses to stressors over which local management strategies have little control (e.g., climate change). Through such actions, MPAs may play a refugial role for marine organisms and help to maintain biodiversity and ecological processes in the face of a changing climate (IUCN World Commission on Protected Areas (IUCN-WPCA) 2008; McLeod *et al.* 2009).

One effect of climate change that is already noticeable is restructuring of marine communities as species begin to shift poleward with increasing ocean temperatures (Harley *et al.* 2006; Johnson *et al.* 2011b). Temperate marine ecosystems, such as the macroalgal forests of Southeast Australia, are already being effected by range shifts of invasive species (e.g., the sea urchin *Centrostephanus rodgersii*) (Steneck *et al.* 2002). Such species are capable of decimating whole kelp communities, turning them to urchin barrens and

consequently removing the habitat that a variety of species rely upon for protection, many of which are economically important taxa (e.g., the spiny rock lobster *Jasus edwardsii*) (Mislan and Babcock 2008). Protecting marine areas mitigates stressors such as recreational activities, pollution, and fishing, resulting in increased population persistence and resilience with climate change within MPAs (Micheli *et al.* 2012).

An important role of MPAs in an era of changing climate is to ensure long-term maintenance of connectivity among populations (Salm *et al.* 2006; Almany *et al.* 2009). Marine park planners should include provision for adequate and ongoing gene flow of key species in the face of increasing anthropogenic stress and habitat fragmentation. Thus, spacing and location of MPAs should reflect the dispersal capabilities of key species (Roberts *et al.* 2003; Shanks *et al.* 2003; Almany *et al.* 2009), such that connectivity and genetic diversity between reserves is maintained. Species dispersal capabilities have been used to infer MPA spacing across a variety of species (Sala *et al.* 2002; Shanks *et al.* 2003; Palumbi 2004).

Dispersal capabilities of macroalgae are variable and difficult to assess directly due to microscopic propagules and multiple life history stages (Kusumo *et al.* 2006). Past research has suggested poor dispersal capabilities due to the small size of propagules and the short time they remain in the water column. Most macroalgal propagules apparently remain suspended in the water column for a few hours to a week, whereas marine animal larvae can survive weeks to months (e.g., fish) (Santelices 1990; Reed *et al.* 1992). Gene flow among macroalgal populations can also potentially be influenced by a variety of factors such as life cycle (Loveless and Hamrick 1984; Palumbi 1994; Coleman and Brawley 2005) and habitat (Billot *et al.* 2003; Kelly and Palumbi 2010).

Most insights into macroalgal dispersal capabilities have been derived from population genetic studies. Quantitatively synthesizing these results through meta-analysis is an important first step toward incorporating macroalgal connectivity into the design or adaptive management of MPA networks.

The presence and nature of a significant relation between gene flow and geographic distance, isolation by distance (IBD), is useful in the context of MPA design because it

focuses attention on the critical issue of protected areas spacing. This information can then be incorporated into marine reserve models to optimise and maintain MPA connectivity and in turn help inform policy managers (Sala *et al.* 2002; Fernandes *et al.* 2005). I conducted the first global meta-analysis of marine macroalgae to test for IBD. I also aimed to establish whether IBD was general across a variety of factors, including habitat, life cycle, higher taxonomic group, and genetic marker type used.

2.3 Methods

To assemble the data set of published studies, I performed a literature search using the Web of Science database (Reuters 2012) in February 2012. I searched for pairwise combinations of the keywords *genetic* and *connectivity* with *algae*. The reference lists of these papers were inspected for relevant studies that may have been overlooked in the original search.

I used a meta-analysis to investigate the influence of various traits and study variables on the presence and slope of isolation by distance. Inclusion criteria for studies were that they reported a correlation coefficient between genetic and geographic distance (r) and a sample size (n). My search resulted in a total of 24 papers. Because some papers included more than one species or discontiguous marine regions, some studies contributed more than one data point, resulting in an overall sample size of 30 data points. The groupings of variables investigated included life cycle (monoecious, dioecious, alternating generations), habitat (intertidal, subtidal), algal division (Rhodophyta, Phaeophyta, Chlorophyta), and the genetic marker type used (AFLP, microsatellite, and RAPD). The latter can affect the outcome of population genetics studies (Whitlock and McCauley 1999; Burridge *et al.* 2004; Weersing and Toonen 2009). I first tested the significance of each grouping on the entire data set (life cycle, habitat, division, and genetic marker), and then examined the relative strength of each variable within these groups (i.e. monoecious vs. dioecious vs. alternating generations, intertidal vs. subtidal, red vs. brown vs. green, and AFLP vs. microsatellite vs. RAPD).

The meta-analysis was undertaken using MetaWin (Rosenberg *et al.* 2000). A random effects model was used to calculate mean effect sizes (Hyatt *et al.* 2003), and bootstrap

resampling procedures were used to determine confidence intervals (Rosenberg *et al.* 2000). A standardized effect size was calculated for each study from the correlation coefficient of IBD and sample size. The total heterogeneity within the data set, Q_{TOTAL} (Hedges and Olkin 1985), was also calculated. Significance values were corrected with sequential Bonferroni adjustments (Rice 1989).

Publication bias can arise when a meta-analysis comprises a large number of studies with significant results as researchers have a tendency to publish significant results over non-significant results (Dickersin 1990; Scargle 2000). This bias was tested for in my meta-analysis with a funnel plot, as well as a test of correlation between effect size and sample size (Spearman's rank correlation) (Begg 1994).

Because many studies did not present *r* and *P* values for tests of IBD and reported only significance, I also examined the presence of IBD with reported F_{ST} values (a measure of genetic differentiation) and the spatial scale of the study. While this is not necessarily as robust as the meta-analysis (e.g., no accommodation of publication bias or effect size), it provides a coarse analysis for a greater number of studies. Although there are limitations when using F_{ST} as an index of genetic differentiation, it is a suitable choice in many situations (Jost 2008; Heller and Siegismund 2009). Using F_{ST} values, I calculated Rousset's distance measure for each study (F_{ST} / (1-F_{ST})) (Rousset 1997) and used this in the correlation. A log (x + 1) of geographic distance was used in this correlation, as multiplicative effects were considered more relevant than additive effects. A transformation of log (F_{ST} / (1-F_{ST})) + 0.05 was also used in the correlation. Inclusion criteria for studies were that they reported an overall F_{ST} value and were published before 2012. A total of 49 papers met these criteria and, because many assessed population structure within subsets of their study range (e.g., on distinct islands) as well as different species within the one study, the sample size for this analysis increased to 101 data points.

2.4 Results

Isolation by distance significantly affected macroalgae genetic connectivity across all studies (Q_{total} = 585.97, df = 29, $P < 0.05$; Table 2.1). Further, the correlation test between genetic and geographic distance showed that a significant positive correlation was evident across the 49 studies (r^2 = 0.127, $P < 0.01$, Fig 2.1). Moreover, IBD was general among macroalgae of different divisions, habitats, life cycles, and studies involving different genetic marker types ($P < 0.05$ in all cases; Table 2.1). A comparison of effect sizes within groupings revealed no significant influence of covariate on IBD prevalence between intertidal and subtidal algae species (P = 0.436), among different life cycles (monoecious, dioecious and alternating generations) (P = 0.506), among the genetic markers used across studies (P = 0.358, AFLP, microsatellite, RAPD), or among algal divisions (P = 0.344) (Table 2.1). This implies that the presence of IBD was independent of the habitat, higher taxa, genetic, and life-cycle divisions examined. A Spearman's rank correlation test showed no effect of publication bias (r_s = 0.012, P = 0.949, Fig 2.2). An F_{ST} in the range of 0.1–0.2 was centered around a geographic scale of 50–100 km (Figure 2.3).

Table 2.1: Heterogeneity of each group of life history variables (habitat, reproduction, marker and division) and of each individual life history variables within groups (subtidal, intertidal, monoecious, dioecious, alternating, AFLP, MSAT, RAPD, red, green and brown) in a meta-analysis of macroalgal population isolation by distance (n = 30 studies).

Group	Q_{TOTAL}	*P*	Variable*	Q_{TOTAL}	*P*
Habitat	27.526	0.436	Subtidal	476.43	<0.01
			Intertidal	327.75	<0.01
Reproduction	26.23	0.506	Monoecious	58.58	<0.01
			Dioecious	357.79	<0.01
			Alternating	292.54	<0.01
Marker	29.050	0.358	AFLP	79.23	<0.01
			MSAT	950.98	<0.01
			RAPD	108.86	<0.01
Division	29.36	0.344	Red	69.95	<0.01
			Green	41.62	<0.01
			Brown	915.18	<0.01
Total data set			all	585.97	<0.01

*Abbreviations: AFLP, Amplified fragment length polymorphism; MSAT, Microsatellite; RAPD, Random amplified polymorphic DNA.

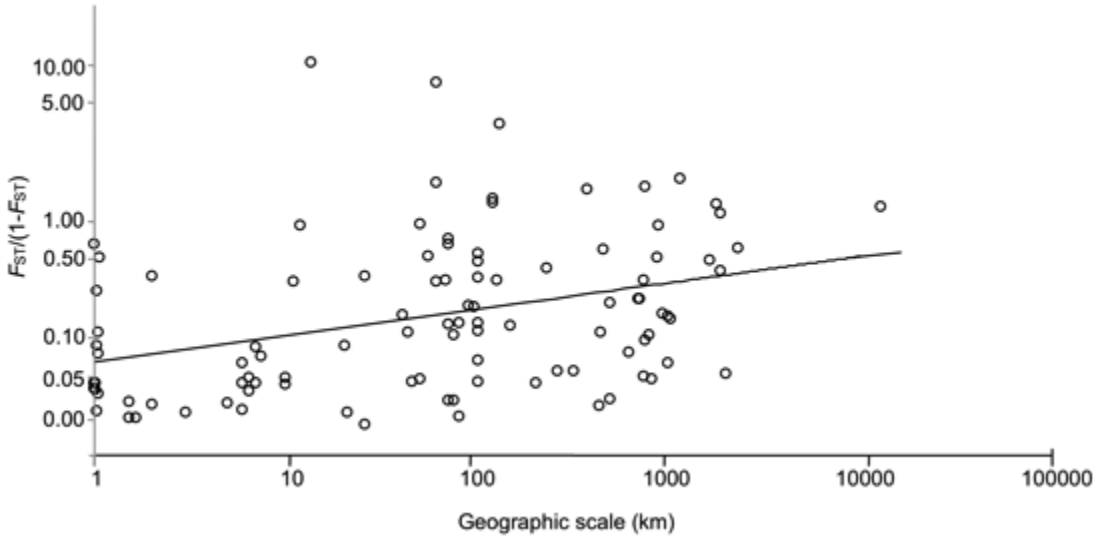

Figure 2.1: Relation between genetic distance, log [(F_{ST} / 1-F_{ST})+0.05], and geographic distance, [log (x+1)] (r^2 = 0.127 P < 0.01) in populations of macroalgae.

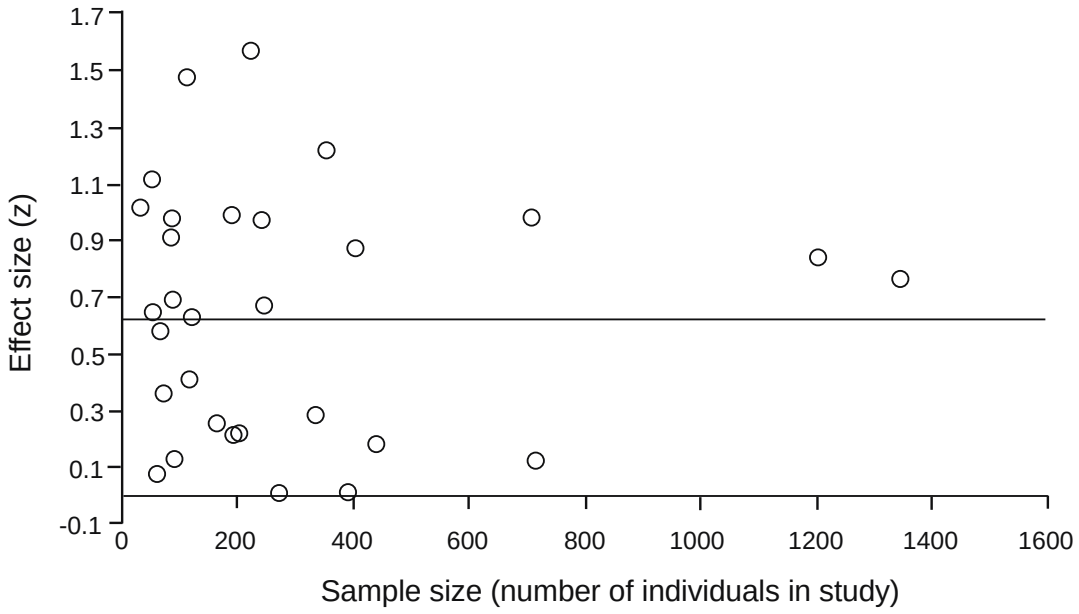

Figure 2.2: Relation between each studies effect size and sample size included in the meta-analysis, testing for publication bias (Pearson's correlation test, r_s=0.012, p=0.949; mean effect size [E=0.6249], horizontal line).

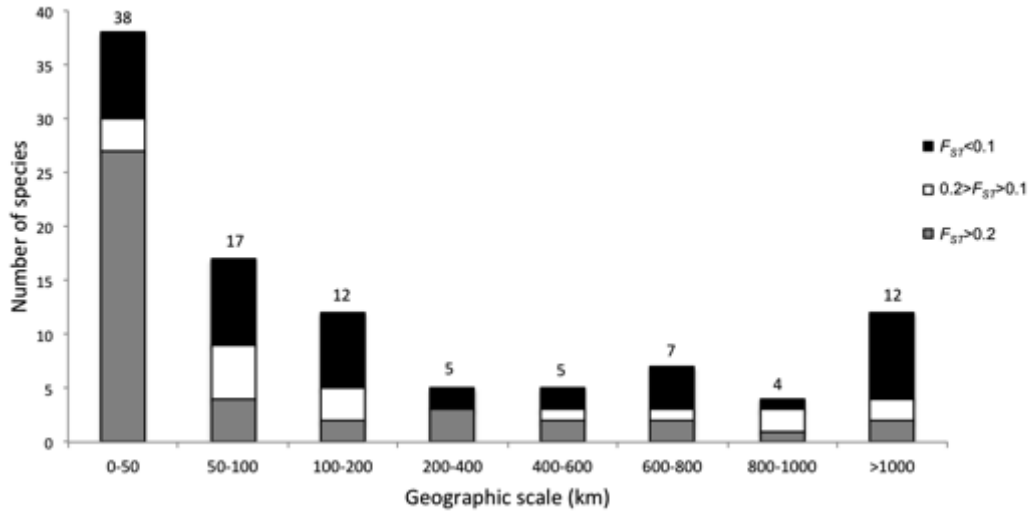

Figure 2.3: Total number of macroalgae species in each three F_{ST} categories (F_{ST} > 0.02, 0.2 > F_{ST} > 0.1, F_{ST} < 0.1) with the corresponding spatial scale (geographic distance category) the study was performed over, to determine the number of studies that had gene flow 0.2 > F_{ST} > 0.1 and at what spatial scales.

2.5 Discussion

Genetic and geographic distance for macroalgae were positively correlated. This correlation was prevalent regardless of macroalgal division, habitat, life cycle, and molecular marker surveyed. Macroalgal propagules are generally broadcast spawned and are relatively immotile (limited endogenous capacity for movement); dispersal distances are determined primarily by ocean currents, wave action, and other physical vectors of dispersal (Reed *et al.* 1992; Gaylord *et al.* 2002; Gaylord *et al.* 2004). Reproduction is also often tightly cued to environmental conditions including calm periods, low tide, or slack tides, which increases fertilization success (Pearson and Serrão 2006) but may reduce variance in dispersal distances. These characteristics, which are seen in many macroalgal species, may explain why I found evidence of IBD across a multitude of studies and species in my meta-analysis.

Isolation by distance should be considered in assessing spacing of MPAs. For example, the slope of the IBD correlation can be used to determine the maximum distance for MPA spacing such that F_{ST} will not exceed a certain magnitude, for example the level that corresponds to approximately one migrant per generation (F_{ST} = 0.2) or any other predetermined level of genetic differentiation. A network of MPAs with individual

protected areas arranged in such a manner to maintain F_{ST} below 0.2 should result in relatively little population differentiation (Slatkin 1987; Wang 2004). The majority of studies I surveyed exhibited $F_{ST} > 0.2$ at spatial scales of less than 50 km (Fig 2.3).

Many studies have used similar distance values to those suggested here (50 km) in MPA planning reports and particle modeling (Roberts *et al.* 2001; Almany *et al.* 2009; California Department of Fish and Game (CDFG) 2009). Studies such as these are theoretically based, with some incorporation of information on larval dispersal distances. I derived similar results based on a synthesis of empirical genetic studies of dispersal distances and population connectivity. This is the first time empirical data for macroalgae has been collated and statistically reviewed in the context of MPA design, an important consideration given the fundamental role that habitat-forming algae play in marine community biodiversity. Similar genetic data exists for a wide range of marine species (Ridgway *et al.* 2008; Curley and Gillings 2009; Schultz *et al.* 2011), and could likewise be incorporated into future planning to achieve more informed decisions that consider connectivity. Recently, the importance of empirical studies in MPA management has been emphasized (Botsford *et al.* 2009).

Meta-analytical approaches have been criticized, including in the MPA literature (Huntington 2011), for failing to account for publication bias, which occurs when primarily positive results are published, providing a biased sample. No significant effect of publication bias was detected in my meta-analysis (Spearman's rank correlation $r_s = 0.012$, $P = 0.949$, Fig 2.2). However, studies frequently neglected to report *r* and *P* values and instead provided a simple statement about whether the IBD was present or absent, a serious failure in statistical reporting (Gerrodette 2011).

The strength of conclusions about source-sink dynamics within MPA networks will be greatly enhanced when different sources of information are cross-validated. In addition to studies of genetic distance, the field of meta-population dynamics has advanced rapidly in recent years through genetic marker studies and greatly improved particle dispersal models. A recent study using genetic parentage analysis for two fish species in the Great Barrier Reef Marine Park, for example, indicated broad scale reseeding of adjacent areas from parents living within no-fishing zones (Harrison *et al.* 2012).

Oceanic particle dispersal modeling provides a further avenue for estimating probabilities of macroalgal gene flow among MPAs and identifying likely source and sink populations (Roberts 1997; Treml *et al.* 2008; Munday *et al.* 2009). Through modeling approaches, temporal heterogeneity in dispersal can also be appreciated through hindcasting (Espíndola *et al.* 2012). Ocean models are, however, rarely accurate in shallow nearshore waters (Roberts 1997; Bode *et al.* 2006) and should be validated with biological data. In combination, genetic distance information, genetic marker information, and oceanic models incorporating seasonal variability and climate change allow key areas for future MPA protection to be identified, ultimately permitting increased species persistence through time (Munday *et al.* 2009).

My finding of an overall pattern of IBD in macroalgae suggests that the spatial distribution of MPAs and unprotected populations is likely to be critical in determining the level of connectivity of macroalgae populations within MPA networks. Given increasing anthropogenic stressors, networks of MPAs should be designed with the intention to maintain dispersal among a network of similar areas and, in addition, serve as sources of genetic material for areas not afforded protection. I found a high proportion of macroalgae displayed $F_{ST} > 0.2$ even at a scale of 0–50 km, indicating that MPA's spaced further than 50 km apart may be susceptible to genetic isolation. This finding is consistent with modeling studies (Roberts *et al.* 2001; Almany *et al.* 2009; Moffitt *et al.* 2011). Data obtained from collating IBD values across a range of species can be incorporated in MPA models and help improve the decision making process for MPA managers. This will contribute to the formation of representative and adequately spaced marine reserve networks.

Acknowledgments

My research was funded by an Australian Research Council Linkage Grant LP100200122 (awarded to GE) and postgraduate scholarship funding from the University of Tasmania.

Chapter 3

Isolation via next generation sequencing of microsatellites from the Tasmanian macroalgae *Lessonia corrugata* (Lessoniaceae)

This chapter is published as:

Durrant H.M.S., Burridge C.P., and Gardner M.G. (2015). Isolation via next generation sequencing of microsatellites from the Tasmanian macroalgae *Lessonia corrugata* (Lessoniaceae). *Applications in Plant Sciences*, 3(7):1500042

3.1 Summary

Microsatellite markers for the macroalgae *Lessonia corrugata* were developed, for the first time, to enable population genetic assessment of this important foundation species. Ion Torrent sequencing identified 16,622 loci, 29 of which were trialled in *L. corrugata*. Seven loci were found to be polymorphic and screened for variation in 76 individuals from two populations in Tasmania, Australia. Observed heterozygosity ranged from 0.086-0.686 (mean 0.386) and the number of alleles per locus ranged from 2 to 5 (mean 2.57). Heterozygosity was not significantly different from expected. These loci can be used to study the population genetics of *L. corrugata*, a key habitat forming species in the Tasmanian marine ecosystem, and will help to assess gene flow among spatially discrete populations such as those in marine protected areas.

3.2 Introduction

Macroalgae provide habitat for many ecological and economically important marine species, supporting highly diverse ecosystems (Wernberg *et al.* 2010). *Lessonia* is one such genus endemic to the Southern Hemisphere (Lane *et al.* 2006). *Lessonia corrugata* (Lucas) is a Tasmanian endemic habitat forming macroalgae found along highly exposed intertidal rocky shorelines (Edgar 1984). Although other *Lessonia* species have been the focus of genetic studies (e.g., Tellier *et al.* 2011), only one of these employed microsatellite markers, and *L. corrugata* has remained relatively understudied in terms of population genetic variation.

All *Lessonia* species possess an alternation of generations life history, which is characterised by two alternating stages, a diploid macroscopic sporophyte stage (the stage of sample collection for this study) and a microscopic gametophyte haploid stage. Dispersal can occur via released gametophytes and by drifting fertile sporophytes that become detached from the substrate during storm events or through herbivory. Although the latter mode of dispersal has greater capacity for long distance transport, *Lessonia* sporophytes are relatively heavy and lack flotation structures, making them unable to float for long periods of time. Their limited capacity for dispersal could mean *Lessonia* has

difficulty recolonising disturbed areas in comparison to other macroalgae species. This makes them suitable candidates for genetic studies on population genetics.

In the age of next generation sequencing, microsatellites remain the most polymorphic and informative genetic marker for inferring species population genetics. Technological advances have now made microsatellite development faster and cheaper with Ion Torrent PGM platforms proving to produce substantially more data at a faster rate and cheaper cost than other sequencing platforms (Elliott *et al.* 2014). Here I use this platform to develop microsatellite markers for *Lessonia corrugata*.

3.3 Methods

Genomic DNA (1µg) was isolated from silica gel dried tissue following the CTAB protocol of Hoarau *et al.* (2007a) with some modifications. Prior to pulverization, microcentrifuge tubes containing tissue and a ball bearing were placed in liquid nitrogen so as to ensure tissue was sufficiently brittle. Instead of incubating and rotating samples at room temperature after the addition of CTAB buffer, samples were incubated at 55°C without rotation. Due to problems encountered with DNA quality, the resulting supernatant from centrifuging samples containing CTAB buffer and chloroform-isoamyl alcohol was first filtered through an Epoch spin column (Epoch Biolabs, Sugarland, TX) and an additional wash step was performed before eluting in Tris-HCl buffer. Throughout the process Epoch spin columns were used instead of making silica fines.

DNA was submitted to the Australian Genome Research Facility (Brisbane node), purified using the Aurora Nucleic Acid Extraction System (Boreal Genomics, Vancouver, BC) and sequenced on an Ion Torrent PGM platform (Life Technologies, Mulgrave, Australia) using a 318 chip with 400 bp chemistry using standard protocols. Shearing of DNA was conducted with a Covaris S2 model (Covaris, Woburn, MA) with shearing parameters slightly modified (Duty Cycle 10%, Intensity 4,100 cycles per burst, 80 sec duration) to provide more DNA fragments in the 350–400 bp range. These fragments were then size selected using a Pippin Prep (Sage Science, Beverly, CA) to ensure the majority of fragment were greater than 300 bp and did not exceed 400 bp. Fragments were tagged by ligating with standard Ion Torrent barcode adaptors. Equal molar ratios of fragments were

mixed prior to sequencing. Post sequencing the fragments were demultiplexed, base called and aligned using Torrent Suite™ Software, which produced 285,231 total reads, with an average read length of 147 bp. I used the program QDD v. 2 (Meglecz *et al.* 2010) to screen the raw sequences for ≥ eight di-, tetra- or penta-base repeats, remove redundant sequences, and design primers from 16,622 possible loci (automated in QDD using Primer3 (Rozen and Skaletsky 1999)).

I followed the procedure outlined in Gardner *et al.* (2011) to choose 29 loci for further development (Table 3.1). The loci were first trialled for PCR amplification in 20 individuals of *L. corrugata* using 1X MyTaq HS Mix (Bioline, Alexandria, Australia), 1µL (20µM) of each forward and reverse locus-specific primer and 1–5 ng/µL DNA in 10µL reactions. The following PCR conditions were used: 95°C for 2 min followed by 25 cycles at 95ºC for 30 sec and 57ºC for 4 min. PCR products were visualised on a 1.5% agarose gel stained with Midori Green. All 29 loci amplified an unambiguous product of the expected size. These amplifiable loci were then tested for polymorphism via capillary electrophoresis. Of the 29 loci, seven (24%) were polymorphic and 22 (76%) were monomorphic in a panel of 20 individuals. Due to the possibility of self-fertlisation in macroalgae species such as *L. corrugata* (Raimondi *et al.* 2004), I ensured testing of loci was conducted on individuals geographically separated from each other by ~8.6 km in order to decrease the chances of monomorphism resulting from clones. Polymorphic loci were then scored in 76 individuals from two populations from Tasmania, Australia: Blessington Point (43°02'15.08"S, 147°24'15.49"E) and Kingston Beach (42°58'29.78"S, 147°20'15.75"E) (Table 3.2). Voucher specimens from Blessington Point (*HO 578210*) and Kingston Beach (*HO 578209*) were deposited in the Tasmanian Herbarium.

Table 3.1. Characteristics of 29 microsatellite loci developed in *Lessonia corrugata*.

Locus	Primer sequence (5'-3')	Repeat motif	Size (bp)	T_a (^oC)	GenBank accession no.
LCO94*	F: ATTCGAACTCGGGACTCCA	$(AC)_{16}$	94	60	KR337302
	R: CTGGATGTCGTTGAGCAGAA				
LCO95*	F: CCGATGAGCAGAAATAACGG	$(AC)_7$	95	600	KR337303
	R: ATTTGGATAAATCGGCTCGC				
LCO96*	F: TGCTGGATGTCGACGAGTAG	$(AC)_7$	96	60	KR337304
	R: CAAGCATAACACGGGTGGAT				
LCO97*	F: CAGTATACGCCAGAGCCACC	$(AC)_8$	97	60	KR337305
	R: TGCTGGATGTCGACGAGTAG				
LCO100*	F: CTGGATGTCGATGAGCAGAA	$(AC)_{10}$	100	60	KR337306
	R: AAGGCTACCCATGCATACGA				
LCO100AG*	F: GTGAGCGCGTCTCCTATGTT	$(AG)_{15}$	100	60	KR337307
	R: TGCGAGCTGGAGATCAACTA				
LCO102	F: TTCGAGTTGCTAGGTACGGC	$(AG)_{16}$	105-107	60	KR337308
	R: CAGCATCGTGCATTGTACCT				
LCO104*	F: AACCACCCAACACGAACAGT	$(AC)_{15}$	104	60	KR337309
	R: CTTGGCTGGATGTCGAGAGT				
LCO146	F: AACACTTTGACCCGACAAGC	$(AC)_9$	149-151	60	KR337310
	R: TGTGCTGGATGTCGATGAGT				
LCO153AGC*	F: GACCAGGGACAAGAAGGGTT	$(AGC)_8$	153	60	KR337311
	R: GATGATACCGTTGCTCCACC				
LCO153AC*	F: GACGCACTGCTGTACGATGT	$(AC)_{10}$	153	60	KR337312
	R: GGGATGAAGAAATCAGCAGG				
LCO154	F: GAGTATATGCGCCAACGTGA	$(AGC)_{10}$	158-161	60	KR337313
	R: GAACACGAGCTGGACGATTC				
LCO158*	F: TTAGAAGTGCATCGTGTCGC	$(AC)_{11}$	158	60	KR337314
	R: GTGTGCTGGATGTCGATGAG				
LCO160*	F: ACTCCGCAGAGTACTGGGAA	$(AC)_{14}$	160	60	KR337315
	R: CGATGAGCAGAAGAACGGAT				
LCO197*	F: GGGTTAAGAACTCTTGCAACTTC	$(AAC)_9$	197	58	KR337316
	R: TTAGCAGCCAACACAAATACAA				
LCO198*	F: TCATCACCGTTATCGTGATATTT	$(AGC)_7$	198	59	KR337317
	R: GAGCGAGAAGTGGAGGGAC				
LCO199	F: TGGAAACCCAATCTCACAAA	$(AGC)_{10}$	201-204	59	KR337318

	R: AACGGTCTTGTGGTCTTTGC				
LCO200*	F: AATTCCCGGTCCCAAGTC	$(AC)_8$	200	60	KR337319
	R: AAGAGTTGATCCGGTGATGC				
LCO205*	F: CAACGGATTATTCTCGGAAGG	$(AG)_{10}$	205	60	KR337320
	R: ACGATAAGCTGCTGGAGGG				
LCO208	F: CTGGATGTCGATGAGCAGAA	$(AC)_{11}$	199-207	60	KR337321
	R: AAGTTGCGTTGGAACCGAT				
LCO217	F: CGAGTAGAAGACGGTTAGTGTGAA	$(AC)_{17}$	222-238	59	KR337322
	R: GCGGCCTATTGTCGTGATA				
LCO222*	F: ACGAAAGAGCGTGGAAACAC	$(AGC)_7$	222	59	KR337323
	R: CGTCTCCTTCGACAGTAGTGA				
LCO223*	F: GCGGCTTGTCTAATGTCATC	$(ACAGT)_7$	223	59	KR337324
	R: CGAGCACCGATCACAAAGTA				
LCO240*	F: GACGAATAATTGATGTTCGAAACTTG	$(AC)_8$	240	61	KR337325
	R: GAATCAGCCACGGACACTG				
LCO241AC10*	F: GTGGAGCCGAAAGGAACAAT	$(AC)_{10}$	241	60	KR337326
	R: CTTTGTGGGTGGTAGCGG				
LCO241AC17*	F: CGAGTAGAAGACGGTTAGTGTGAA	$(AC)_{17}$	241	59	KR337327
	R: ACACAAGTTAAGAAATAGGCAACTG				
LCO245*	F: GATCATCTCGAGCCTCGTCT	$(AGC)_6$	245	60	KR337328
	R: CAGATGACCGGTGCGTTC				
LCO251	F: TTTGTTTCTGCAATGCTTCG	$(AT)_9$	254-260	60	KR337329
	R: AGAAGCGCTATCATGCTGGA				
LCO252*	F: AAGAGGTCACACGGGAGATG	$(AT)_6$	252	60	KR337330
	R: CTATCGAACCTGACAAGCCG				

Note: * = monomorphic loci

Table 3.2. Genetic variation of the seven polymorphic loci in *Lessonia corrugata*.

	Blessington Point (n = 41)				Kingston Beach (n = 35)						
Locus	A	H_o	H_e	p	A	H_o	H_e	p	N_A	PIC	F (null)
LCO102	2	0.108	0.102	0.728	2	0.457	0.496	0.640	2	0.328	0.196
LCO146	2	0.366	0.481	0.125	2	0.257	0.337	0.162	2	0.369	0.214
LCO154	2	0.268	0.232	0.550	2	0.486	0.420	0.002	2	0.336	0.368
LCO199	3	0.390	0.366	0.541	3	0.600	0.599	0.517	3	0.455	0.051
LCO208	2	0.268	0.299	0.512	2	0.500	0.479	0.046	2	0.289	0.136
LCO217	4	0.585	0.583	0.137	5	0.686	0.670	0.820	5	0.599	0.005
LCO251	3	0.350	0.434	0.396	2	0.086	0.082	0.791	3	0.274	0.113

Note: A = number of alleles, H_o = observed heterozygosity, H_e = expected heterozygosity, *P* = *P*-values obtained from Hardy-Weinberg equilibrium tests, n = number of individuals tested, N_A = total number of alleles, PIC = polymorphic information content, *F* (null) = null allele frequency

I used MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004) to check each locus for evidence of null alleles, scoring error due to stuttering, and large allele drop-out. For each locus I calculated the number and size range of alleles, observed and expected heterozygosity, and tested conformance to Hardy-Weinberg Equilibrium (HWE) using GenAlEx (Peakall and Smouse 2006; Peakall and Smouse 2012). Polymorphic information content was calculated using CERVUS 3.0.7 (Kalinowski *et al.* 2007). I also checked all pairs of loci for linkage disequilibrium in GENEPOP and adjusted for multiple tests of significance using FDR (Benjamini and Yekutieli 2001).

3.4 Results

Observed and expected heterozygosity ranged from 0.086–0.686 (mean 0.386) and 0.082–0.67 (mean 0.398) respectively, with the number of alleles per locus ranging from 2 to 5 (mean 2.57) (Table 3.2). Two loci (LCO154 and LCO208) were significantly different from HWE in the Kingston Beach population but not in the Blessing Point population (Table 3.2). No individuals were found to be genetically identical. There was no evidence for null alleles, large allele drop out, or scoring error due to stuttering ($P > 0.05$) (Table 3.2). There was no evidence for linkage disequilibrium after adjusting for multiple tests ($P > 0.05$, 21 tests).

3.5 Conclusions

Using the Ion Torrent platform I identified 29 microsatellite loci, of which seven were polymorphic. Cross-amplification in 11 taxonomically accepted species in the *Lessonia* genus may be possible. In addition the markers developed here will be used to document the population genetics of *L. corrugata* and investigate the influences of habitat patchiness on genetic structure. Understanding the processes that affect gene flow in this habitat forming species will contribute towards conserving populations and consequently protecting the biodiversity of the marine ecosystems this macroalgal species supports.

Chapter 4

The influence of habitat on population connectivity in the macroalgae *Lessonia corrugata* (Lessoniaceae)

This chapter is currently in preparation:

Durrant, H.M.S., Barrett, N.S., Edgar, G.J. and Coleman, M.A., and Burridge, C.P. (in prep). The influence of habitat on population connectivity in the macroalgae *Lessonia corrugata* (Lessoniaceae).

4.1 Summary

Macroalgal populations provide important habitat for a suite of marine organisms, supporting highly diverse ecosystems. However, these macroalgal populations are now under threat from climate change, anthropogenic disturbance and invasive species, all of which are causing a decrease in macroalgal abundance and geographic range. Marine Protected Areas (MPAs) are used to protect marine communities by mitigating threats from anthropogenic activities. Although previous studies have investigated the degree of connectivity between networks of MPAs, they have not considered the influence of intervening habitat on population connectivity, and therefore their inferences cannot be used to inform MPA design in other areas. Understanding how habitat influences connectivity is vital to the success of MPAs and conservation strategies such as translocations, as population connectivity is essential for the exchange of genes and maintenance of ecosystem resilience. Seascape genetics considers the spatial structuring of habitat and environmental variables to understand their influence on population genetic structure and population connectivity, and can identify habitat types that represent barriers to dispersal as well as regions of conservation priority for marine reserves.

Here I conducted a seascape genetics study to investigate the influence of intervening habitat (sand, reef and open water) and hydrological processes (particle dispersal probability models) on the dispersal of the macroalga *Lessonia corrugata* in the Derwent Estuary, Tasmania. Dispersal in *L. corrugata* was limited across large stretches of open water, and between populations separated by large geographic distances. The proportion of intervening habitat represented by sand was negatively correlated with population connectively, and conversely, the proportion of reef was positively correlated with population connectivity. Furthermore, particle dispersal probability models only appeared to explain population connectivity when population comparisons across stretches of open water were included in the analysis. My results will help to inform appropriate MPA design, and direct marine translocation strategies to successfully maintain population connectivity and ecosystem resilience.

4.2 Introduction

Population connectivity is an important aspect of conservation biology, as it allows the exchange of genes between populations, maintaining genetic variability and population resilience through the retention of advantageous genotypes (Salm *et al.* 2006; Almany *et al.* 2009). In times of stress, from environmental or anthropogenic disturbance, individuals residing within affected populations are able to disperse away from disturbed regions into more advantageous habitats if populations are connected sufficiently to allow dispersal. In addition to allowing dispersal away from disturbed habitats, population connectivity also allows individuals to recolonise nearby areas that may have been negatively affected by anthropogenic disturbance and environmental stressors (Coleman *et al.* 2011a). Without connectivity and gene flow, population's risk reduced genetic variability and an increased risk of extinction due to an absence of advantageous genotypes to adapt to climatic changes (Reed 2005).

Marine Protected Areas (MPAs) are used to protect areas of conservation significance, decreasing disturbance from fishing and recreational and commercial activities (Hoegh-Guldberg 2004; Fernandes *et al.* 2005; Jones *et al.* 2007). However, the continued success of these reserves relies on their ability to not only protect populations, but to maintain population connectivity (Palumbi 2003; Fernandes *et al.* 2005; Jones *et al.* 2007). Although previous studies into MPA connectivity have been able to determine how well existing networks of MPAs maintain genetic connectivity (e.g., Coleman *et al.* 2011a), such studies are case specific and tend not to pursue habitat or environmental causality, and as such cannot guide MPA design in other areas. "Seascape genetics" (the marine incarnation of "landscape genetics") assesses the influence of environmental variables on population connectivity (Manel *et al.* 2003; Selkoe *et al.* 2008). Inferences from seascape genetics studies can thus inform the optimum placement of MPAs to ensure connectivity among populations in areas outside the study region, provided the availability of environmental data for such regions exists. Similarly, seascape genetics studies can identify instances where population connectivity may only be maintained via individual translocations.

Macroalgal populations support highly diverse marine ecosystems, through functioning as foundation species, providing habitat for a variety of marine taxa of both economical and ecological significance (Mann 1973; Dayton 1985; Edyvane 2003). However, with increasing anthropogenic disturbance, climate change and invasive species, the abundance and geographic range of macroalgal species has decreased, posing a threat to temperate marine biodiversity (Valentine and Johnson 2004; Johnson *et al.* 2005; Ridgway 2007). Despite these impending threats to macroalgal communities, few studies have used seascape genetics to better understand macroalgal dispersal (although see Alberto *et al.* 2011; Brennan *et al.* 2014). A potential impediment to seascape genetics is that marine habitats are more difficult to map than terrestrial environments, although advances in remote sensing and mapping technologies, and increases in community surveys (e.g., Ierodiaconou *et al.* 2007; Wright and Heyman 2008; Edgar and Stuart-Smith 2014), are now making it easier to obtain spatial data on marine habitats. The accuracy of particle dispersal modelling to estimate population connectivity can also be tested in seascape genetic studies (e.g., Coleman *et al.* 2011b; Coleman *et al.* 2013). However, particle dispersal models tend to fail when applied to nearshore species, because shallow depth causes complex interactions between waves, sediment transport and turbulence, which cannot be accurately predicted by modelling (Alberto *et al.* 2011).

The lower Derwent Estuary in southern Tasmania provides an opportunity to determine how habitat variables influence gene flow of marine macroalgae. The shorelines of the lower estuary are characterised by continuous patches of rocky reef with intervening stretches of sand, and deep water between adjacent shores, allowing the replication of both sand and rocky reef habitat types between sites in seascape genetic analyses. In the lower reaches, the estuary is fully marine. A high-resolution particle dispersal model also exists for this region (Condie *et al.* 2005; http://www.csiro.au/connie2/), which considers factors such as tidal flux, wind forcing, seasonality and depth to generate an informed set of probability statistics for particles dispersing between locations. Additionally, because tides dominate particle dispersal in the estuary on short time scales (i.e., hours to days) within the estuary, any influence they could have on individual dispersal will be accurately modelled (Herzfeld *et al.* 2005; Whitehead *et al.* 2010).

Lessonia corrugata Lucas, a habitat-forming macroalga endemic to Tasmania, occupies subtidal rocky shorelines with moderate wave exposure. Its reproductive life history is characterised by alternation of generations, where microscopic gametophytes alternate with macroscopic sporophytes. Within this life history, dispersal can occur at three points. Firstly, spores released from the adult sporophyte disperse throughout the water column for a matter of hours to days before settling upon the substrate (Santelices 1990). From here they develop into dioecious gametophytes. Secondly, gametophytes produce gametes (sessile eggs and motile sperm). These gametes have poorer dispersal capabilities than spores, and additionally require fertilisation for dispersal to be realised (Luning and Muller 1978; Maier *et al.* 1988; Reed *et al.* 1992). Once fertlisation has occurred an adult sporophyte develops in the location where the female gametophyte was situated. Finally, fertile sporophytes can become detached from the substrate through either herbivory or storm activity, and disperse via currents, potentially releasing viable spores en route (Macaya *et al.* 2005; Hernandez-Carmona *et al.* 2006).

Although sporophytes have great dispersal potential in many macroalgae (Dayton 1985; Smith 2002), *L. corrugata* lacks gas filled bladders that aid in buoyancy (Dayton 1985; Koehl 1986; Tellier *et al.* 2009). Additionally, *L. corrugata* is also well adapted to exposed rocky shorelines, and as such has developed strong and heavy holdfasts that cause it to sink. Therefore, *L. corrugata* has limited sporophyte dispersal capability (Dayton 1985; Macaya *et al.* 2005; Muhlin *et al.* 2008). Although previous studies of *Lessonia* species have used population genetic markers to quantify population connectivity (e.g., Martinez *et al.* 2003; Faugeron *et al.* 2005), none to date have explicitly used seascape genetics to better understand how environmental variables influence dispersal, or have investigated *L. corrugata*. In this study I investigate the influence of intervening habitat and currents on dispersal of *L. corrugata* in the Derwent Estuary. I focused on *L. corrugata* as it is an endemic species with limited range, an important component of nearshore ecosystems, and one likely to have limited dispersal capability due to its life history and morphology.

4.3 Methods

4.3.1 Sample collection and DNA extraction

Lessonia corrugata were sampled from 14 intertidal locations in the Derwent Estuary, Tasmania, in May 2014 (Figure 4.1, Supplementary Table S3). At most locations approximately 15 individuals were collected in each of three clusters that were separated by a minimum of 30 m (approximately 45 individuals in total per location). Genomic DNA was isolated from silica gel dried tissue following the CTAB protocol of Hoarau *et al.* (2007a) with some modifications. Prior to pulverisation, microcentrifuge tubes containing tissue and a ball bearing were placed in liquid nitrogen so as to ensure tissue was sufficiently brittle. Instead of incubating and rotating samples at room temperature after the addition of CTAB buffer, samples were incubated at 55°C without rotation. Due to problems encountered with DNA quality, the resulting supernatant from centrifuging samples containing CTAB buffer and chloroform-isoamyl alcohol was first filtered through an Epoch spin column (Epoch Biolabs, Sugarland, TX) and an additional wash step was performed before eluting in Tris-HCl buffer. Epoch spin columns were used throughout the process rather than making silica fines.

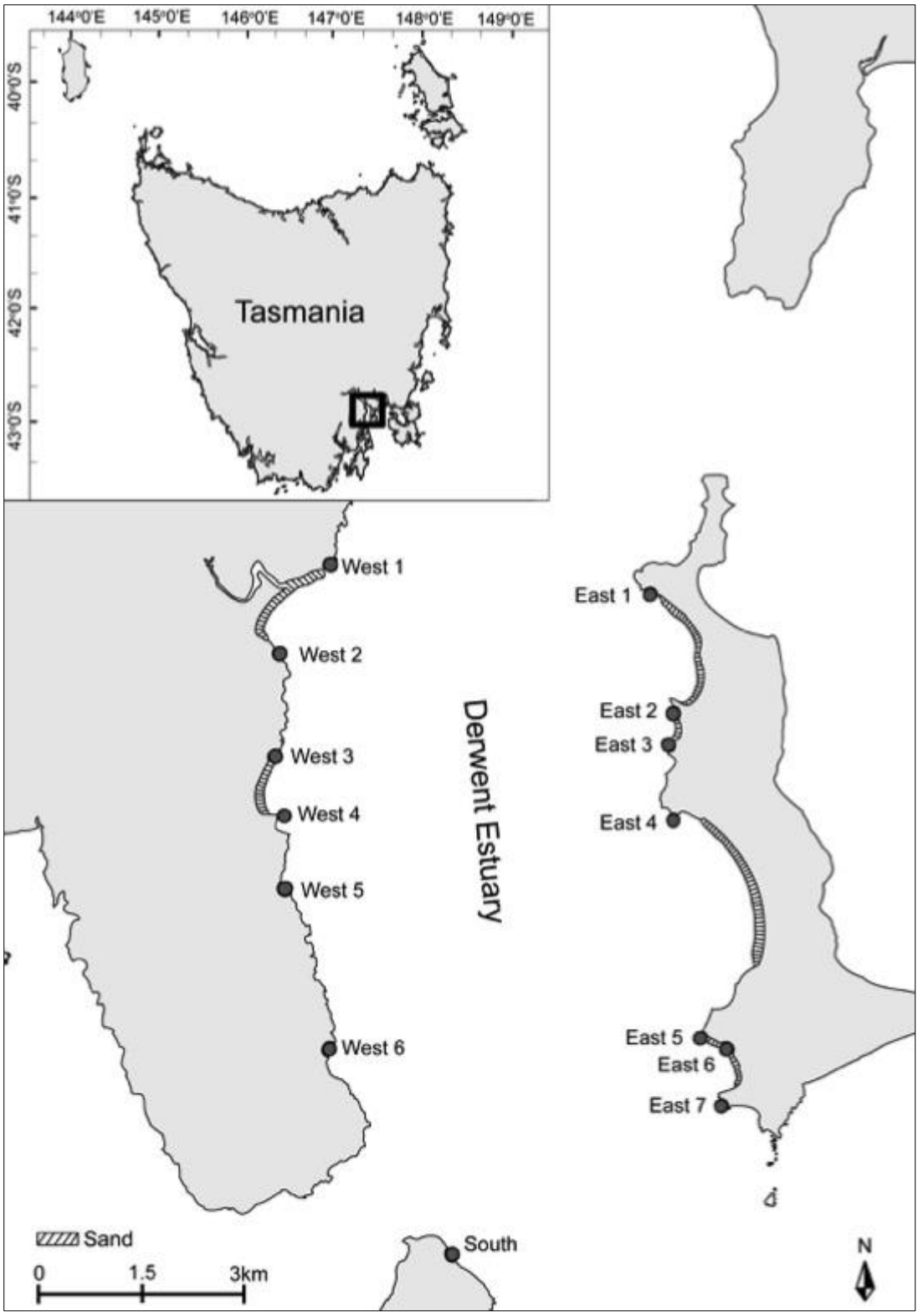

Figure 4.1: Sampling locations of *Lessonia corrugata* in the Derwent Estuary. Shorelines between sampling sites are rocky reef except where otherwise indicated.

4.3.2 Microsatellites and PCR protocol

Seven polymorphic microsatellite loci designed by Durrant *et al*. (2015b) were scored for 562 individuals over the 14 sampling locations. Genotyping was carried out at the Australian Genome Research Facility (AGRF). PCR amplification was performed using 1X MyTaq HS Mix (Bioline, Alexandria, Australia), 0.5 µM of each forward and reverse primer, and 50 ng DNA in 10 µL reactions. The following PCR conditions were used: 95°C for 2 min followed by 25 cycles at 95ºC for 30 sec and 57ºC for 4 min. PCR products were separated on an ABI 3130 and sized relative to GS500.

4.3.3 Descriptive genetic analysis

For each locus I tested for evidence of null alleles, scoring error due to PCR stuttering, and large allele dropout using MICROCHECKER 2.2.3 (Van Oosterhout *et al.* 2004). Observed (H_o) and expected (H_e) heterozygosities were calculated in GenAlEx (Peakall and Smouse 2006; Peakall and Smouse 2012). Conformance of loci to Hardy-Weinberg Equilibrium (HWE) and linkage disequilibrium were assessed using GENEPOP (Raymond and Rousset 1995; Rousset 2008) with significance adjusted for multiple tests using False Discovery Rate (FDR) (Benjamini and Yekutieli 2001). Inbreeding coefficients (F_{IS}) were calculated using GENODIVE (Meirmans and Van Tienderen 2004).

4.3.4 Tests of population structure

Pairwise F_{ST} values for populations and exact tests of allele frequency homogeneity were calculated using GENODIVE. Correlations between genetic and geographic distance (Isolation by Distance) were tested with the Isolation by Distance Web Service (IBDWS) (Jensen *et al.* 2005) using linearized F_{ST} values (F_{ST} / 1-F_{ST}) and minimum marine distance between localities measured using Google Earth 7.1, which were then log-transformed in accordance with Rousset (1997). Reduced Major Axis Regression was performed to describe the relationship as this method accounts for the error in sampling independent variable x. Population structure was assessed under Bayesian clustering using STRUCTURE 2.3.4 (Pritchard *et al.* 2000) with 100 000 Markov chain steps under the admixture model. *K* (number of potential clusters) ranged from 1 to 14, with 20 replicate analyses for each value. Optimal number of clusters was guided using Δ*K* (Evanno *et al.* 2005) in

STRUCTURE HARVESTER (Earl and vonHoldt 2012), and CLUMPP (Jakobsson and Rosenberg 2007) was used to collate all runs produced by STRUCTURE for a given value of *K*. Results were then visualised using DISTRUCT (Rosenberg 2004). An analysis of multidimentional scaling (MDS) was performed for both F_{ST} and particle dispersal matrices using R (R Development Core Team 2014). As this analysis accepts dissimilarity matrices only and cannot accept zero values in matrices, particle dispersal probabilities were converted to (1-probability). GENALEX was used to calculate hierarchical Φ-statistics by performing an Analysis of Molecular Variance (AMOVA). These Φ-statistics were calculated for three groupings: among shores (east vs. west + south), among locations (the 14 sampling sites), and within locations (the three samples within each site).

4.3.5 Quantifying intervening habitat

The proportion of intervening habitat, comprising reef, sand and open water (deeper then the euphotic zone, as *L. corrugata* is limited beyond this region), between all sampling locations was determined using the geographic information system ArcGIS v10.3, utilising available habitat data from Seamap Tasmania (http://seamap.imas.utas.edu.au/), in addition to Google Earth 7.1. As sand and reef are mutually exclusive, the proportion of reef and open water between locations were employed for seascape genetic analysis (if these two are specified, sand comprises the remainder). The probability of particle dispersal between sites was determined with Aus-Connie (Condie *et al.* 2005; http://www.csiro.au/connie2/). Propagules were released at each sampling location at a depth of 2 m, with a dispersal period of 2 days, as individuals are frequently observed at these depths within the estuary, with spore viability limited to hours–days (Santelices 1990). I then determined the probability of each location acting as a source for all other locations. At the time of analysis this model had a resolution 500 m^2 and was only able to function for a maximum period of 19 days (20/1/2010–7/2/2010). Given the short dispersal times of spores (Santelices 1990; Reed *et al.* 1992), it is most likely that tidal fluxes influence spore dispersal, which tend not to differ considerably between seasons. Therefore the time period used was considered sufficient to capture potential influences of particle dispersal on genetic structure. Dispersal of propagules between some locations was bidirectional; in this situation the maximum probability of dispersal between two locations was used in subsequent analyses (Supplementary Table S4) (see Alberto *et al.* 2011).

4.3.6 Seascape genetic analysis

Although the field of seascape genetics is growing, the discipline has primarily developed within the terrestrial literature (landscape genetics). Traditionally landscape genetics has employed Mantel and partial Mantel tests to assess correlations of genetic differentiation with habitat variables. However, both Mantel and partial Mantel tests exhibit elevated type I error rates and inflated correlation values in landscape genetic analyses and are therefore not appropriate when assessing multiple explanatory variables and multiple tests simultaneously (Balkenhol *et al.* 2009; Legendre and Fortin 2010). As IBDWS uses a traditional Mantel test, the influence of distance on genetic structure was also later tested using models that better account for the non-independence of pairwise distances. Mantel tests are now being replaced by multiple alternatives, 11 of which were compared and tested by Balenhol *et al.* (2009). Three methods showed a suitable level of power and reduced type-I error rate: Canonical Correspondence Analysis (CCA), Multiple Regression of Distance Matrices (MRDM) and Bayesian Inference of Immigration Rates (BIMR). Since this review an additional test for landscape genetic analysis has been promoted by Van Strien *et al*. (2012); a Linear Mixed Effects (LME) modelling approach, estimated via Maximum Likelihood Population Effects (MLPE) (Clarke *et al.* 2002), was found to provide accurate inferences about influential habitat types and population genetic variation. The use of R^2_β (Edwards *et al.* 2008) rather than the traditional R^2 value also provided a more realistic measure of model fit, as it does not increase simply because an additional predictor variable has been added to a model. Additionally, the use of traditional AIC values is also shown to be inappropriate for LME methods, as these values can be influenced by the non-independence of predictor variables (Clarke *et al.* 2002). These advancements in landscape genetic statistical analyses provide the opportunity to make ecologically meaningful inferences regarding a species' genetic structure.

The influences of intervening habitat type, minimum marine distance, and probability of particle dispersal on F_{ST} were evaluated using a Linear Mixed Effects model based on a Maximum Likelihood Population Effects approach, as outlined by Van Strien *et al*. (2012). Analyses were performed in the LME4 package in R (R Development Core Team 2014). This method is useful for landscape genetic analysis as it accounts for non-independence of

pairwise comparisons, and has the ability to cope with the correlative nature of explanatory habitat variables. In order to determine the linear model that best explained variation in F_{ST} I compared all possible combinations of explanatory variables using R^2_β as a measure of model fit (Edwards *et al.* 2008). This measure was calculated using the PBKRTEST package (Halekoh and Hojsgaard 2014) in R, and was employed because it is not susceptible to inflation with the addition of predictor variables, and provides a more realistic measure of model fit than traditional AIC values in these analyses.

While methods exist for estimating recent gene flow that also lack certain equilibrium assumptions, when trialed on this dataset they were either inappropriate with respect to assumptions regarding levels of gene flow and sample size (Faubet *et al.* 2007; Meirmans 2014), or failed to converge (Faubet and Gaggiotti 2008). Therefore, Fst was employed as the response variable, and this is a common practice in landscape genetics, and while more simulation studies are required, Fst appears to approach equilibrium more rapidly then other metrics (Epps and Keyghobadi 2015).

4.4 Results

Mean number of alleles per locus at a location ranged from 2.00–2.71, and observed and expected heterozygosity ranged from 0.152–0.487 (mean 0.379) and 0.145–0.483 (mean 0.397) respectively (Table 4.1). Genotypes at all loci were within Hardy-Weinberg equilibrium ($P > 0.05$) and there was no evidence of linkage disequilibrium ($P > 0.05$). MICROCHECKER suggested null alleles were present at loci Lco102, Lco217, Lco146, Lco199 and Lco154; however inferences were inconsistent across populations and all loci were retained in subsequent analyses.

Table 4.1: Genetic variation of 14 populations of *Lessonia corrugata*. *n* = number of individuals genotyped, N_A = mean number of alleles per locus over all loci ± SE, H_o = observed heterozygosity, H_e = expected heterozygosity, and F_{IS} = multi-locus inbreeding coefficient.

Site	*n*	N_A	H_o	H_e	F_{IS}
West 1	35	2.57 ± 0.429	0.435	0.431	0.006^{ns}
West 2	42	2.43 ± 0.297	0.447	0.453	0.024^{ns}
West 3	40	2.57 ± 0.297	0.428	0.468	0.097*
West 4	45	2.57 ± 0.429	0.437	0.454	0.047^{ns}
West 5	47	2.71 ± 0.421	0.455	0.476	0.062^{ns}
West 6	45	2.57 ± 0.429	0.461	0.473	0.037^{ns}
East 1	43	2.57 ± 0.297	0.368	0.365	0.004^{ns}
East 2	43	2.29 ± 0.184	0.280	0.350	0.212**
East 3	44	2.00 ± 0.309	0.152	0.145	-0.042^{ns}
East 4	37	2.14 ± 0.261	0.207	0.233	0.124^{ns}
East 5	41	2.57 ± 0.297	0.327	0.351	0.081^{ns}
East 6	15	2.14 ± 0.143	0.382	0.397	0.072^{ns}
East 7	41	2.43 ± 0.202	0.450	0.474	0.063^{ns}
South	45	2.71 ± 0.421	0.487	0.483	0.004**

Note: Significance values indicated as *($P < 0.01$) **($P < 0.005$), ns = not significant.

There was a significant relationship between genetic and geographic distance ($r^2 = 0.059$, $P = 0.008$, Figure 4.2), although it appeared mostly due higher genetic difference being associated with between-shore comparisons, which were also the more geographically isolated. AMOVA revealed significant structuring among shores ($\Phi_{RT} = 0.100$, Table 4.2) and among locations ($\Phi_{SR} = 0.095$, Table 4.2). F_{IS} values indicated possible non-random mating at some locations (Table 4.1), and may account for the high and significant Φ_{ST} value ($\Phi_{ST} = 0.186$, Table 4.2) that indicated non-random structuring of genetic variation within locations (based on the within location subsamples). Pairwise F_{ST} estimates between locations on the western shoreline were smaller in comparison to those on the eastern shoreline (Figure 4.2, Table 4.3). All western sites also displayed lower pairwise F_{ST} values with the southern site (south) compared to pairwise comparisons between eastern sites and south (Figure 4.2, Table 4.3). Finally, all F_{ST} estimates between pairs of sites on eastern and western shorelines were relatively high (Figure 4.2, Table 4.3). STRUCTURE showed that the data were best explained under a *K* value of 2, whereby all

western sites and south grouped together separately from all eastern sites (Figure 4.3, Supplementary Figure S1). When K = 3, further structuring can be observed in locations situated along the eastern shoreline (Supplementary Figure S2). Results from MDS analyses of F_{ST} showed clear groupings between the western and eastern shore locations, with the southern site grouping with all western locations (Figure 4.4(a)). When particle dispersal probabilities were used in MDS analyses this grouping became even clearer, with obvious distinction between eastern and western shorelines, and again the southern sampling location grouping with western shore locations (Figure 4.4(b)).

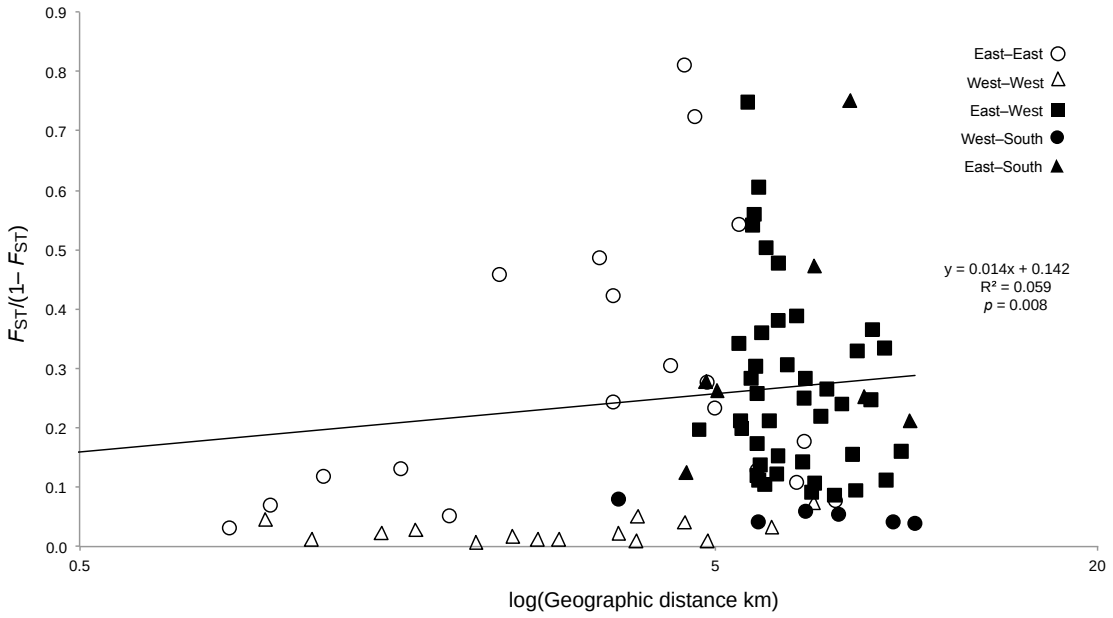

Figure 4.2: Isolation by distance analysis using linearised F_{ST} values (F_{ST} / (1-F_{ST})) and log-transformed minimum marine geographic distances. Each comparison between locations from different shores is indicated by corresponding symbols found in the legend.

Table 4.2: Analysis of Molecular Variance (AMOVA), where 'shores' refers to the grouping of shorelines based on STRUCTURE results (total 2) and 'locations' refers to the 14 sampling locations.

Source of variation	df	variance	% variation	Φ-statistics
Among shores (east vs. west + south)	1	0.18	10.01	$\Phi_{RT} = 0.100$*
Among locations (within regions)	12	0.16	8.59	$\Phi_{SR} = 0.095$*
Within locations	1110	1.49	81.40	$\Phi_{ST} = 0.186$*
Total	1123	1.83		

Note: Significance values indicated as *($P < 0.005$).

Table 4.3: Pairwise F_{ST} estimates among localities (lower diagonal) with corresponding exact test *P*-values (above the diagonal).

	West 1	West 2	West 3	West 4	West 5	West 6	East 1	East 2	East 3	East 4	East 5	East 6	East 7	South
West 1	0	0.001***	0.084^{ns}	0.001***	0.086^{ns}	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
West 2	0.023*	0	0.001***	0.035*	0.091^{ns}	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
West 3	0.011^{ns}	0.028*	0	0.001***	0.105^{ns}	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
West 4	0.049**	0.012^{ns}	0.044**	0	0.042*	0.006**	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
West 5	0.009^{ns}	0.009^{ns}	0.007^{ns}	0.011^{ns}	0	0.008**	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
West 6	0.069**	0.032**	0.040**	0.022*	0.017*	0	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
East 1	0.165**	0.166**	0.095**	0.132**	0.124**	0.134**	0	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
East 2	0.175**	0.148**	0.100**	0.121**	0.109**	0.084**	0.050**	0	0.001***	0.001***	0.001***	0.001***	0.001***	0.001***
East 3	0.428**	0.377**	0.359**	0.351**	0.335**	0.280**	0.314**	0.184**	0	0.001***	0.001***	0.001***	0.001***	0.001***
East 4	0.323**	0.276**	0.265**	0.221**	0.233**	0.175**	0.196**	0.116**	0.106**	0	0.001***	0.001***	0.001***	0.001***
East 5	0.268**	0.248**	0.209**	0.220**	0.234**	0.255**	0.098**	0.217**	0.448**	0.327**	0	0.001***	0.001***	0.001***
East 6	0.250**	0.198**	0.194**	0.180**	0.200**	0.205**	0.150**	0.189**	0.420**	0.297**	0.056*	0	0.023*	0.001***
East 7	0.138**	0.100**	0.087**	0.080**	0.096**	0.107**	0.071**	0.113**	0.352**	0.233**	0.065**	0.030^{ns}	0	0.001***
South	0.038**	0.039**	0.051**	0.056**	0.041**	0.075**	0.175**	0.201**	0.429**	0.321**	0.217**	0.208**	0.111**	0

Note: Significance values indicated as *($P < 0.05$) **($P < 0.01$), ***($P < 0.001$), ns = not significant after correction for False Discovery Rate.

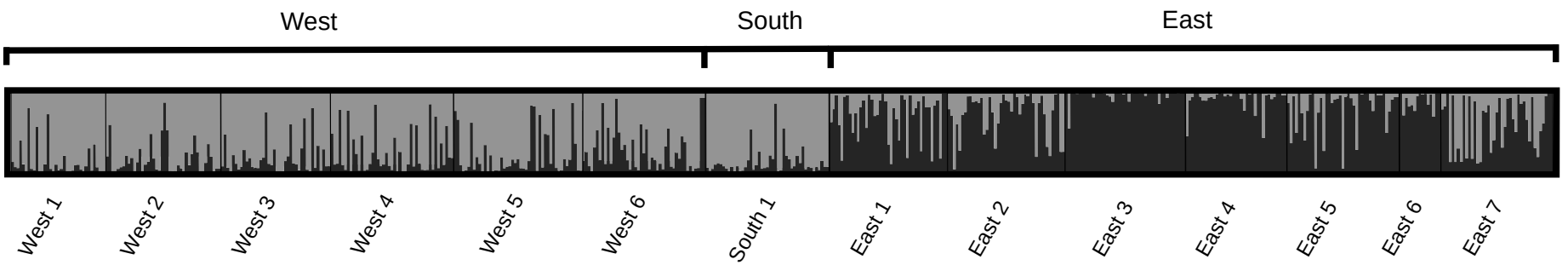

Figure 4.3: Results from STRUCTURE analysis, showing $K = 2$ clusters. Each bar represents an individual within a location, with each colour shade representing the coancestry coefficient of that individual belonging to a particular cluster.

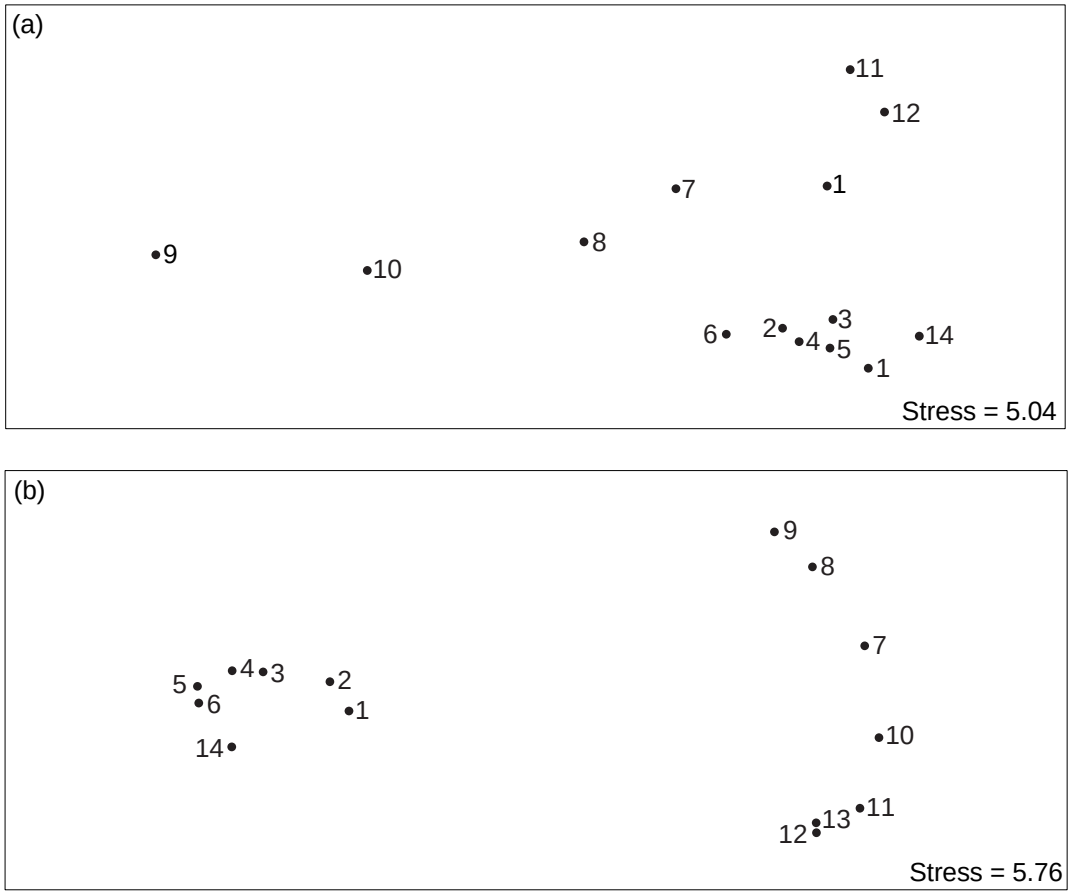

Figure 4.4: MDS plots of *Lessonia corrugata* using a) F_{ST} matrix and b) particle dispersal matrix. Numbers correspond to site locations.

Particle dispersal simulations indicated no dispersal between eastern and western shorelines (Supplementary Table S4, Supplementary Figure S3). All locations situated along the western shoreline acted as a source for all other western locations, albeit at low probabilities. Dispersal between locations on the eastern shoreline appeared to be more restricted than that of western locations (Supplementary Table S4, Supplementary Figure S3). Greater dispersal was observed between western populations and the southern location compared to eastern locations and the southern location (Supplementary Table S4, Supplementary Figure S3).

The full LME model found all explanatory variables significantly influenced genetic structure in *L. corrugata* (Table 4.4). In this model the proportion of reef and open water was negatively correlated with genetic structure, as was the probability of particle dispersal (Table 4.4). Minimum marine distance was positively correlated with genetic structure.

Due to the mutually exclusive nature of sand and reef, the proportion of sand between sites was significantly positively correlated with genetic structure. R^2_β values were consistently high among all models (0.408–0.454) except those lacking open water and reef (Table 4.4). Open water and reef were found to have high R^2_β values when analysed individually (0.408 and 0.432 respectively, Table 4.4) in comparison to minimum marine distance and particle dispersal probability (0.088 and 0.133 respectively, Table 4.4). Correlation coefficients indicated a strong negative correlation between open water and reef (r = -0.89), and a moderate negative correlation between open water and minimum marine distance (r = -0.61), and open water and probability of particle dispersal (r = -0.48). Furthermore, when analysed separately, the proportion of open water was significantly positively correlated with genetic structure, whereas in the full LME model it was significantly negatively correlated with genetic structure. The full model result for open water is presumably due to its correlations with other explanatory variables.

Table 4.4: Results from LME (linear mixed effects) for all models with pairwise between-shore site comparisons and for the full model excluding all between-shore comparisons and open water.

Model	R^2_β	Intercept ($\times 10^{-1}$)	Open water ($\times 10^{-1}$)	Reef ($\times 10^{-1}$)	Minimum distance ($\times 10^{-5}$)	Particle dispersal probability ($\times 10^{-2}$)
Full	0.446	2.18***	-0.62*	-1.98***	0.69*	-0.11*
Model 1	0.454	1.74***	-0.45^{ns}	-1.80***	1.09***	–
Model 2	0.427	2.53***	-4.90^{ns}	-1.99***	–	-0.20***
Model 3	0.422	0.99*	0.56***	–	0.70*	-0.08^{ns}
Model 4	0.426	1.69***	–	-1.15***	0.55^{ns}	-0.09*
Model 5	0.435	2.10***	-0.06^{ns}	-1.69**	–	–
Model 6	0.429	0.74*	0.61***	–	1.02^{ns}	–
Model 7	0.402	0.13***	0.70***	–	–	-0.10**
Model 8	0.429	1.42**	–	-1.19***	0.94**	–
Model 9	0.417	2.06***	–	-1.31***	–	-0.10***
Model 10	0.141	0.98*	–	–	1.32***	-0.11*
Model 11	0.408	1.13**	0.92***	–	–	–
Model 12	0.432	2.05***	–	-1.61***	–	–
Model 13	0.088	0.62*	–	–	1.83***	–
Model 14	0.133	1.79***	–	–	–	-0.20***
			Removal of between-shore comparisons		($\times 10^{-1}$)	
Full	0.237	1.53*		-2.62**	3.62**	39.0^{ns}

* Note: '–' indicates that this variable was excluded. Significance values indicated as *($P < 0.05$) **($P < 0.01$) ***($P < 0.001$), ns = not significant.

Given that the strongest genetic structuring appeared associated with comparisons involving open water (F_{ST} and STRUCTURE), in addition to the strength of the correlations between open water and other explanatory variables, I excluded these between-shore comparisons (and hence open water) to more rigorously assess the influence of the remaining explanatory variables on genetic structuring. The resulting model that excluded open water (between-shore) comparisons showed that particle dispersal probability no longer explained genetic structure (Table 4.4), while the proportion of reef and minimum marine distance were significantly negatively and positively correlated with genetic structure, respectively (Table 4.4). Concomitantly, the proportion of sand was significantly positively correlated with genetic structure. This model had a lower R^2_β value (0.237, Table 4.4) than the original full model (0.446, Table 4.4), however the two significant explanatory variables were not substantially correlated (r = -0.026), unlike those in the original full model.

4.5 Discussion

Despite the fine geographic extent (approximately 10 km) of the study area, significant genetic structuring was encountered in *Lessonia corrugata*. All explanatory variables were found to significantly influence genetic structure according to the full LME model: proportion of open water and reef, minimum marine distance, probability of particle dispersal. However, due to correlations between the proportion of open water and all other explanatory variables, these inferences were potentially confounded. Therefore, all site comparisons involving open water were removed, and an additional LME analysis was performed. The resulting model showed both proportion of reef (and concomitantly sand) and minimum marine distance significantly influenced genetic structure, with the proportion of reef negatively correlated with genetic structure, while the proportion of sand and minimum marine distance were positively correlated with genetic structure. Particle dispersal probability did not significantly explain observed genetic structure in this reduced model. As this reduced model lacked substantial correlations among predictors, its inferences regarding these variables are more reliable than the full model.

The fine geographic scales of genetic structuring in *L. corrugata* (< 800 m) are consistent with prior suggestions that *Lessonia* species have limited dispersal capabilities (Dayton

1985; Santelices 1990). This scale of genetic structuring is also similar, if not smaller, than observed for other macroalgae (e.g., Wright *et al.* 2000; Faugeron *et al.* 2001; Zuccarello *et al.* 2001; Coleman *et al.* 2011a). One macroalga to show particularly fine (down to 5 m) spatial genetic structuring is the intertidal *Postelsia palmaeformis* (Ruprecht), and this was explained by poor dispersal capabilities of both spores and rafting adult plants (lacking floatation structures) (Kusumo *et al.* 2006). Similarly, *L. corrugata* is unlikely to disperse widely as drifting adults, and produces spores with poor dispersal capabilities (Norton 1992). These factors presumably play a large role in the fine spatial scale of significant genetic structuring observed.

4.5.1 Distance and habitat

Geographic distance between populations of marine species is known to be an important factor in structuring population genetic variation (e.g., Durrant *et al.* 2014; Wright *et al.* 2015). Furthermore, some studies have indicated a relationship between marine habitat and genetic structure. For example, Riginos and Nachman (2001) found that genetic structure in the obligate rocky reef fish *Axoclinus nigricaudus* increased when sand dominated intervening habitat in comparison to when rocky reef dominated intervening habitat. Given that *L. corrugata* is an obligate rocky reef species, it is not surprising that the proportion of sand and open water between sites was positively correlated with genetic structure, and the proportion of reef was negatively correlated. Regions of deep open water (deeper then the euphotic zone) pose as unsuitable habitats for a variety of taxa, and have been shown to restrict dispersal in marine species such as corals (Ayre and Hughes 2004), fish (Riginos and Nachman 2001; Zhi-Qiang *et al.* 2015) and gastropods (Hoffman *et al.* 2011a; Hoffman *et al.* 2011b). Moreover, studies of several marine invertebrate species indicate that the influence of habitat on genetic structure is affected by whether a species is a habitat generalist or specialist, and have found habitat generalists were more likely to traverse potential barriers to gene flow such as sandy beaches, whereas habitat specialists (such as obligate rocky reef species) relied on the presence of specific intervening habitat types as stepping-stones for dispersal (Ayre *et al.* 2009). However, alternative situations may exist where connectivity may actually be greater across regions comprising unsuitable habitat, as a species may continue to move, in contrast to movement within suitable

habitat, which may be more restricted given recruitment will be successful (e.g., Simpson *et al.* 2014).

4.5.2 Particle dispersal modelling

The full LME model indicated that particle dispersal probability was significant and negatively correlated with genetic structuring. However, particle dispersal probability was moderately correlated with the proportion of open water between sites, and did not significantly explain genetic structuring where open water was absent between sites. Therefore, while previous studies that have found particle dispersal probability to be significantly negatively correlated with macroalgal genetic structure (Alberto *et al.* 2011; Coleman 2013; Brennan *et al.* 2014), I did not obtain conclusive support for this relationship. It is possible that the 500 m^2 resolution of the Aus-Connie model was too coarse to significantly explain patterns of genetic structure along a shore within this species, due to the hydrological complexities of the shallow environments inhabited by *L. corrugata*. Additionally, this model may not be capable of bottom-water tracking, which is predominately where *L. corrugata* individuals reside once detached from the substrate, due to their negative buoyancy. Improved model resolution may result in greater predictive capabilities of genetic structure in subtidal macroalgae. Reduced sample size for the within-shore analysis may have also reduced power to detect an influence of hydrological processes on connectivity and genetic structure, but could be tested by analysing more sites from within one shore.

Differences in species dispersal capabilities due to morphological characteristics may determine how well particle dispersal models predict genetic structure. Macroalgae possessing flotation structures are capable of dispersing across large geographical distances (e.g., Billot *et al.* 2003; Coleman and Kelaher 2009; Macaya and Zuccarello 2010b; Durrant *et al.* 2015a). While drifting, these species would encounter large-scale oceanographic currents that are more readily modelled. Therefore, buoyant macroalgae may be more likely to exhibit relationships between particle dispersal probability and genetic structuring than species with negative buoyancy such as *L. corrugata*, even if dispersal in the later is indeed significantly influenced by hydrology. Particle dispersal models may therefore prove to be most useful in estimating dispersal capabilities of

macroalgae whose life history and morphology are well adapted to long-range dispersal (e.g., Muhlin *et al.* 2008; Alberto *et al.* 2011; Brennan *et al.* 2014), but not as useful in explaining the genetic structure of species with short-range dispersal capabilities as they may be less likely to encounter hydrological features that are more readily modelled.

4.5.3 Future directions

Although *L. corrugata* shows limited dispersal in comparison to species whose morphology facilitates long distance dispersal (e.g., *Macrocystis pyrifera*) (Dayton 1985; Koehl 1986; Smith 2002; Tellier *et al.* 2009), this could reflect differences in habitat (e.g., depth) rather than species morphology, and analyses of additional species from a range of habitats and morphologies are required to establish whether this is a general trend. Invasive species may also potentially act as barriers to dispersal, monopolising habitat and preventing colonisation of native species (pre-emptive competition; Valentine and Johnson 2004; Johnson *et al.* 2005). Through incorporating the proportion of intervening habitat occupied by invasive species into LME models, we can also understand how invasive species influence the population genetic structure of native species. Furthermore, anthropogenic stressors could also be included in models to determine how species dispersal is influenced by human mediated disturbances.

4.6 Conclusions and conservation significance

My study contributes important knowledge on the factors influencing population connectivity in macroalgae, which are relevant to the design of conservation strategies such as MPAs and translocations. Firstly, I found that dispersal was limited across large stretches of open water (deeper than the euphotic zone), as well as between populations separated by greater geographic distances. Secondly, intervening nearshore habitat (sand/reef) also proved to be an important factor in shaping the population genetic structure of *L. corrugata*. Lastly, particle dispersal modelling might be more useful for understanding genetic structure at larger spatial scales in highly dispersive macroalgae. Locations of marine reserves will influence *L. corrugata* population connectivity. Generally, reserves should not be constructed without consideration of intervening habitat, as this will influence the dispersal of individuals among protected areas. In addition to

informing appropriate MPA planning strategies, my results can also guide translocation strategies. With anthropogenic stressors and future climate change, marine communities are at risk of substantial population declines. Translocations across physical barriers may be required to move individuals in response to disturbances and maintain gene flow to prevent inbreeding depression (e.g., *Phyllospora comosa*; Campbell *et al.* 2014). Knowledge about habitat types that influence dispersal and gene flow will be vital in determining when and where to translocate individuals. Overall, my study revealed significant genetic structure among populations of *L. corrugata* within a southeast Australian estuary and demonstrated the importance of incorporating multiple explanatory variables into seascape genetic analyses.

Acknowledgements

The authors thank Nicole Burtt from the Australian Genome Research Facility, Justin Hulls from the Institute for Marine and Antarctic studies, and Scott Condie from CSIRO for assistance and support. This project was funded by the Holsworth Wildlife Research Endowment and the Australian Research Council LP 100200122.

Chapter 5

Shallow phylogeographic histories of key species in a biodiversity hotspot

This chapter is published as:

Durrant, H.M.S., Barrett N.S., Edgar, G.J., Coleman M.A., and Burridge C.P. (2015). Shallow phylogeographic histories of key species in a biodiversity hotspot. *Phycologia* 54 (6): 556–565.

5.1 Summary

Biodiversity hotspots may result from the retention of lineages through past climatic changes, local diversification of lineages, or the accumulation of lineages derived from elsewhere. Different phylogeographic structuring is anticipated for taxa derived under these scenarios. Here I examine phylogeographic variation in four macroalgae that are dominant in a marine biodiversity hotspot, and provide habitat for a range of other taxa, potentially influencing their diversity as well. Samples of *Ecklonia radiata* (Phaeophyceae), *Macrocystis pyrifera* (Phaeophyceae), *Phyllospora comosa* (Phaeophyceae) and *Lessonia corrugata* (Phaeophyceae) collected from 34 sites in Southeast Australia – a recognised temperate marine biodiversity hotspot – were sequenced for the chloroplast Rubisco spacer region (*rbc*L) and mitochondrial cytochrome *c* oxidase subunit I (COI). Phylogeographic variation was limited to single shallow breaks within *E. radiata* and *L. corrugata*, corresponding to a recognised transition between biogeographic provinces, while *P. comosa* and *M. pyrifera* lacked spatial variation. The limited phylogeographic variation observed, in conjunction with phylogenetic relationships to other populations or congeneric species, suggest that each of these dominant habitat-forming species are recent arrivals (<3 Mya) into the biodiversity hotspot. This contrasts starkly with expectations that dominant taxa in hotspots should reflect lineages that have adapted and persisted in these environments, and raises concerns for the future of these ecosystems under climate change scenarios.

5.2 Introduction

Biodiversity 'hotspots' have been the focus of many terrestrial and marine phylogeographic studies, due to the high levels of speciation and endemism that they can exhibit, and their high conservation significance (Myers *et al.* 2000; Kareiva and Marvier 2003; Carnaval *et al.* 2009). These hotspots can represent areas where lineages have persisted through recent periods of climate change (Carnaval *et al.* 2009; Qu *et al.* 2014), accumulated through population isolation and divergence (Fjeldså *et al.* 2012; Payo *et al.* 2013; Demos *et al.* 2014), or invaded from elsewhere (Barber *et al.* 2011). Phylogeographic structuring of taxa within biodiversity hotspots can be used to distinguish these alternatives, as recently invading and therefore mobile taxa are expected to exhibit

temporally shallower and spatially coarser phylogeographic structuring than lineages that have been abundant within the hotspot for longer periods, and that may have – and continue to be – diversifying as a result of isolation among populations.

Temperate Australia is recognised as a biodiversity hotspot for marine organisms, including fishes, seagrasses and macroalgae (e.g., O'Hara and Poore 2000; Phillips 2001; Roberts *et al.* 2002; Waters 2008; Richardson *et al.* 2009). The magnitude of biodiversity in this region may reflect a variety of factors. First, the region comprises the longest temperate coastline in the world, which in itself provides greater opportunity for the isolation and diversification of lineages. Secondly, it is bordered by three boundary currents, and these vary in temperature, strength and direction (Figure 5.1) (Cresswell and Vaudrey 1977; Mata *et al.* 2006; Middleton and Bye 2007), and may uniquely impact the isolation of lineages (Bennett and Pope 1953; O'Hara and Poore 2000). Finally, historical biogeographic breaks like the Bassian Isthmus, a land bridge that once connected Tasmania to mainland Australia (Lambeck and Chappell 2001; Burridge *et al.* 2004), may have also allopatrically isolated marine lineages (Figure 5.1).

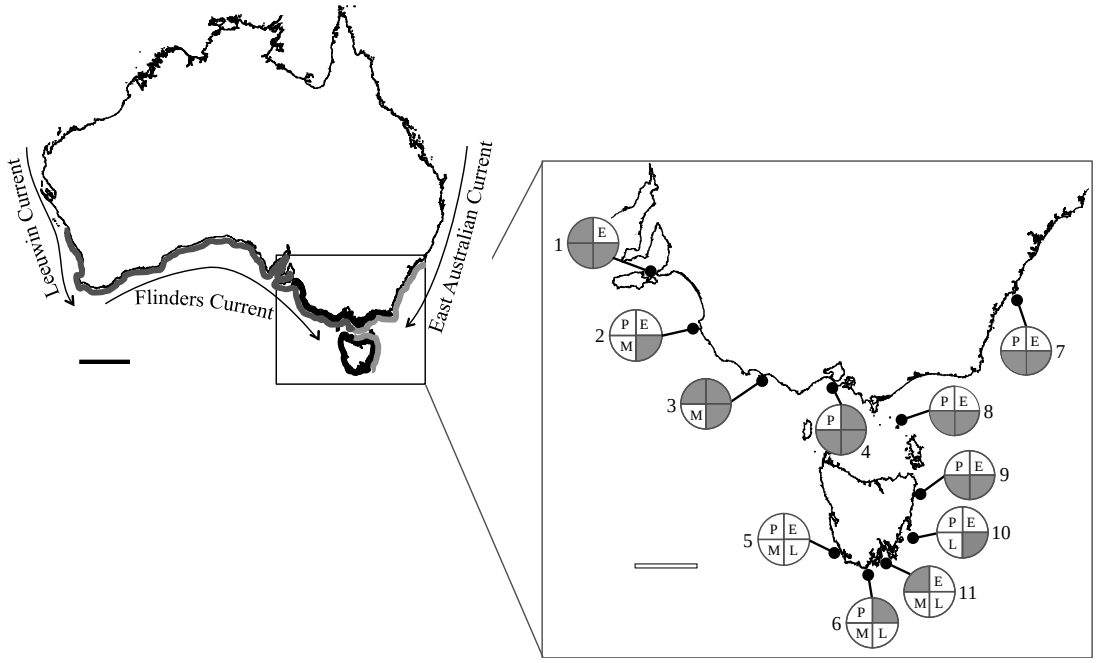

Figure 5.1: Map of Australia showing boundary currents; biogeographic provinces, Flindersian (dark grey) Maugean (York *et al.*) and Peronian (light grey), from Bennett and Pope (1953), and sample locations. Letters in pie charts refer to the species of macroalgae collected from each location, E: *Ecklonia radiata*, L: *Lessonia corrugata*, M: *Macrocystis pyrifera* and P: *Phyllospora comosa*. Each location was sampled at three sub-locations, fully described in supplementary information (Table S3). Black scale bar = 500 km, white scale bar = 200 km.

The potential significance of these explanations is illustrated by the fact that three biogeographic provinces are recognised within this region: Flindersian (west), Peronian (east) and Maugean (south-east) (Bennett and Pope 1953; Millar 2007; Shepherd and Edgar 2013) (Figure 5.1). Patterns of species diversity and range have been found to uniquely correspond to these provinces due to the habitat and environmental heterogeneity between them (Sanderson 1997; Waters *et al.* 2010). Phylogeographic breaks in widespread taxa may also be expected to be coincident with these provincial boundaries, as the same factors influencing the distribution of taxa may also influence the distribution of lineages within taxa (Waters *et al.* 2004; Novaes *et al.* 2013; Villamor *et al.* 2014).

Southern Australia harbours the highest diversity (~1150 species) (Bolton 1994) of temperate marine macroalgae in the world, and has a rich flora of brown algae, comprising at least 230 species (Womersley 1987). A lack of major extinction events is thought to be

an important contributor to their biodiversity (Phillips 2001), as is also suggested for some tropical terrestrial biodiversity hotspots (Gaston 2000; Rull 2006), and can be reflected by high levels of intraspecific genetic variation (Hewitt 2004). However, the phylogeographic history of macroalgae in the Southern Australia region remains understudied relative to the marine fauna (although see Fraser *et al.* 2009c). Several macroalgal species play significant roles in habitat formation and as foundation species (Dayton 1985), supporting highly diverse marine communities (Wernberg *et al.* 2010) and providing refuges for many ecological and economically significant species (Tsukidate 1984; Coleman and Williams 2002; Marzinelli *et al.* 2014). Therefore, an understanding of the processes leading to macroalgal diversity may also explain the biodiversity of co-habiting taxa.

Within southeast Australia four key habitat-forming macroalgae occupy high priority in ecological studies and surveys (Edyvane 2003; Irving *et al.* 2004). Three of these are *Macrocystis pyrifera* (L.) C.Agardh, *Ecklonia radiata* (C.Agardh) J.Agardh and *Lessonia corrugata* Lucas, which are all members of the order Laminariales and possess an 'alteration of generations' life history between macroscopic diploid sporophytes and microscopic haploid gametophytes. The other dominant species is *Phyllospora comosa* (Labillardière) C.Agardh, a member of order Fucales, which possesses a uniphasic dioecious life history. These species also exhibit a range of morphological features likely to influence dispersal potential and phylogeographic structuring. Both *M. pyrifera* and *P. comosa* have gas filled bladders that facilitate flotation, enabling long distance dispersal of sporophytes (Dayton 1985). In comparison, both *E. radiata* and *L. corrugata* lack these features, with *L. corrugata* particularly well adapted to anchoring on exposed rocky shores, possessing a strong and heavy holdfast (Koehl 1986). Population genetic structure of each of these species, or congeners in the case of *L. corrugata*, indicate spatially restricted gene flow (e.g., Coleman *et al.* 2009; Tellier *et al.* 2009; Alberto *et al.* 2010), such that the presence and spatial scale of phylogeographic structuring is logical to test in these Southern Australian macroalgae.

The aim of this study is to expand upon existing knowledge by increasing intraspecific sampling and assessing the phylogeographic histories of these four dominant macroalgal species in temperate Australia. As these are dominant species in a biodiversity hotspot, I expect to find a lack of phylogeographic breaks and a lack of spatial genetic structuring

(e.g., Kieswetter and Schneider 2013; Alvarez-Presas *et al.* 2014). However, existing knowledge of the phylogeographic history of two of these macroalgal species (*Macrocystis pyrifera* and *Ecklonia radiata*) show these species are likely to be recent arrivals into the Southern Hemisphere given that Northern Hemisphere populations tend to display greater genetic variation (Coyer *et al.* 2001; Shepherd and Edgar 2013).

5.3 Methods

5.3.1 Sample collection and DNA extraction

Samples were collected throughout southeastern Australia, encompassing regions under the influence of different boundary currents on either side of the historical Bassian Isthmus land bridge, and from within the Flindersian, Maugian, and Peronian biogeographic provinces (Figure 5.1, Table S1). Five individuals of each species were sequenced per site within each location, and depending on the location the samples were preserved in ethanol on site or placed on ice, rinsed with freshwater and preserved in silica gel. In some locations not all four species were present or able to be collected due to logistic constraints (Figure 5.1).

DNA extraction followed the CTAB protocol of Hoarau *et al.* (2007a) with some modifications. Prior to pulverizing, microcentrifuge tubes containing tissue and a ball bearing were placed in liquid nitrogen so as to ensure tissue was sufficiently brittle for pulverizing. Instead of incubating and rotating samples at room temperature after the addition of CTAB buffer, samples were incubated at 55°C without rotation. Due to problems encountered with DNA quality, the resulting supernatant from centrifuging samples containing CTAB buffer and chloroform-isoamyl alcohol was first filtered through an Epoch spin column (Epoch Biolabs, TX, USA) and the wash step was duplicated before eluting in Tris-HCl buffer. Throughout the process Epoch spin columns were used instead of silica fines.

Previously described mitochondrial and chloroplast molecular markers were amplified for each species. Plastid markers were chosen as they undergo lineage sorting four-times faster than nuclear DNA markers, and therefore will provide finer resolution of genealogical relationships (Avise 2009). Primer pairs for the mitochondrial cytochrome *c* oxidase

subunit I (COI) region, chloroplast Rubisco spacer region (*rbc*L) and respective PCR conditions were as follows: GazF1/R1 (Saunders 2005), *Phyllospora comosa* and *Macrocystis pyrifera*; GazF2/R2 (Lane *et al.* 2007), *Ecklonia radiata* and *Lessonia corrugata*; rbc68F/708R (Silberfeld *et al.* 2010), *E. radiata, L. corrugata* and *M. pyrifera*; and KL2/KL8 (Lane *et al.* 2006), *P. comosa*.

5.3.2 Statistical methods

Haplotype (*H*) and nucleotide (π) diversities were calculated for each species and marker using DnaSP version 5.0 (Rozas and Rozas 1995) (see supplementary Table S6 for a complete list of GenBank accession numbers). Rarefaction curves were employed during comparisons among species to accommodate differences in sample sizes, using the vegan statistical package in R 3.0.3 (R Development Core Team 2014). Haplotype median-joining networks (Bandelt *et al.* 1999) were reconstructed using PopArt (http://popart.otago.ac.nz/index.shtml), and analysis of molecular variance (AMOVA) were performed using Arlequin version 3.0 (Excoffier *et al.* 2005) to quantify partitioning of genetic variance within and among sampling localities. These Φ-statistics were calculated for each marker type (mtDNA/cpDNA) that showed haplotype variation, within each respective species. A spatial analysis of molecular variance (SAMOVA) was also performed using samova version 1.0 (Dupanloup *et al.* 2002) to identify the clustering of localities into groups that best explained the spatial distribution of molecular variance.

5.4 Results

5.4.1 Haplotype and nucleotide diversity

Phyllospora comosa lacked variation for both mitochondrial and chloroplast markers (Figure 5.2). All other species exhibited variation at the mitochondrial marker, but *Ecklonia radiata* was the only species to exhibit variation at the chloroplast marker (Figure 5.2). Where polymorphisms existed, haplotype diversity was much greater than nucleotide diversity (0.262–0.634 and 0.00043–0.00491 respectively; Figure 5.2), indicating only small nucleotide differences between haplotypes. All rarefaction curves showed that the total number of haplotypes observed is equal to asymptotic values (Figure 5.3). This

indicates that despite differences in sample size among taxa, the number of haplotypes has not been underestimated.

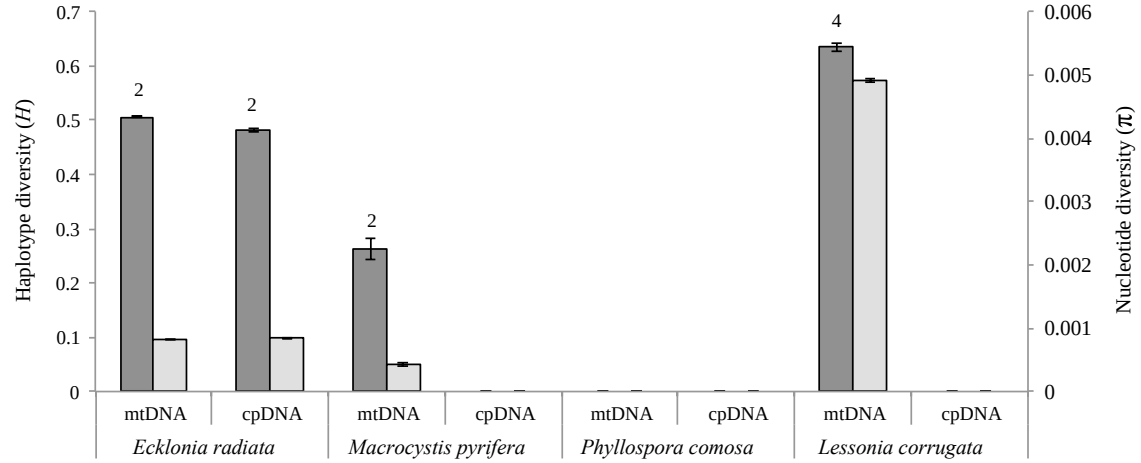

Figure 5.2: Haplotype (*H*, grey columns) and nucleotide diversities (π, white columns) diversities for mitochondrial (mtDNA) and chloroplast (cpDNA) markers for each macroalgal species. Sample sizes: *Ecklonia radiata* (mtDNA: 80, cpDNA: 67) *Macrocystis pyrifera* (mtDNA: 27, cpDNA: 41), *Phyllospora comosa* (mtDNA: 75, cpDNA: 79) and *Lessonia corrugata* (mtDNA: 39, cpDNA: 40). Values shown above bars indicate number of haplotypes for given marker.

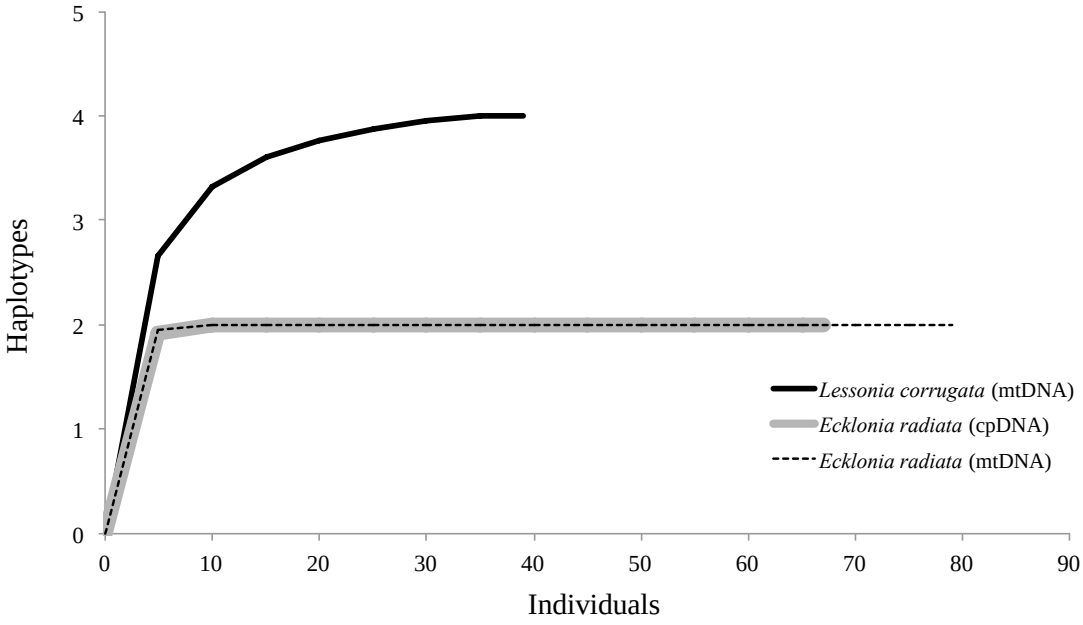

Figure. 5.3: Rarefaction curves for all populations of *Lessonia corrugata* (mitochondrial marker), and *Ecklonia radiata* (mitochondrial andchloroplast markers), demonstrating that the maximum number of haplotypes present in these samples is likely to have been encountered.

5.4.2 Networks

The *E. radiata* chloroplast marker exhibited two haplotypes, with one being restricted to western locations and the other restricted to eastern locations (Figure 5.4(a)). On the other hand the mitochondrial marker showed no such east-west differentiation between *E. radiata* populations, for example the eastern geographic location 7 grouped with the eastern locations 1, 2 and 5, possibly reflecting chance fixation of ancestral polymorphism (Figure 5.4(b)). *Lessonia corrugata* exhibited four spatially restricted mitochondrial haplotypes (Figure 5.4(c)), with one haplotype observed in the south and southwest of Tasmania, while the other three were restricted to the Tasmanian east coast sample locations, with all three at one sample site, and the other two represented at single sites. *Macrocystis pyrifera* exhibited two mitochondrial haplotypes, but one of these was only found at one site (Figure 5.4(d)). As above, *Phyllospora comosa* showed no haplotypic variation at either marker. Sampling locations corresponding to each relative haplotype are shown in Figure 5.4(e).

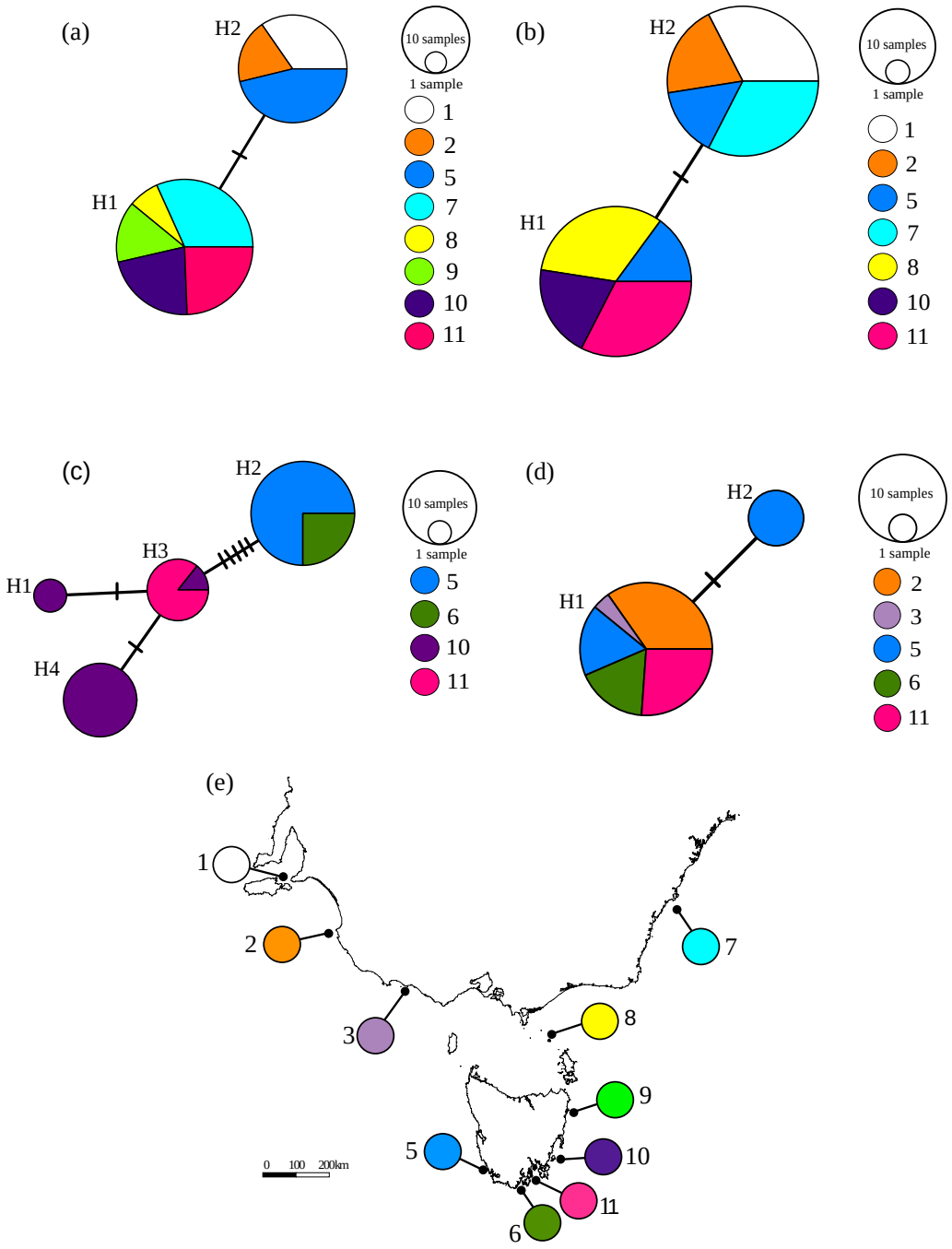

Figure 5.4: Haplotype networks. Each colour is a unique geographic location, circle size is proportional to sample size, straight lines represent single base pair mutations and dashes indicate inferred (unsampled) haplotypes: a: *Ecklonia radiata* (cpDNA), b: *Ecklonia radiata* (mtDNA), c: *Lessonia corrugata* (mtDNA), d: *Macrocystis pyrifera* (mtDNA) and e: map displaying sample locations corresponding to relative colour in the haplotype networks.

5.4.3 AMOVA

For *E. radiata* 100% of chloroplast and 85.68% of mitochondrial genetic variance occurred among populations (Φ_{ST} = 1.00, P < 0.05; Φ_{ST} = 0.86, P < 0.05, respectively). Only 36.13% of mitochondrial variance was observed among *M. pyrifera* populations (Φ_{ST} = 0.36, P < 0.05). Finally 83.51% of mitochondrial genetic variance in *L. corrugata* was observed among populations (Φ_{ST} = 0.84, P < 0.05).

5.4.4 SAMOVA

SMOVA suggested the presence of two groups for *E. radiata* and *L. corrugata* mtDNA given the rapid attainment of asymptotic Φ_{CT} (supplementary Figure S4). *Macrocystis pyrifera* (mtDNA) and *Ecklonia radiata* (cpDNA) both produced a maximum Φ_{CT} of 1 at two groups (supplementary Figure S4).

5.5 Discussion

The physical isolation of the Australian continent along with a perceived lack of mass extinction events has been invoked to explain its high temperate macroalgal species diversity and endemism (Phillips 2001; Kerswell 2006). However, under these circumstances a high level of haplotype variation would be expected in temperate Australian macroalgae, as observed for other taxa distributed in biodiversity hotspots (e.g., Lawson 2013; Alvarez-Presas *et al.* 2014), and spanning multiple biogeographic provinces (Villamor *et al.* 2014). Instead, there are low levels of genetic variation within the species I surveyed, on both molecular and spatial scales. These results contrast with observations for marine animals in this region that exhibit phylogeographic structuring on a range of spatial and temporal scales. For example, the round herring (genus *Etrumeus*), showed genetic structure corresponding to the historical Bassian Isthmus biogeographic break and the temperate biogeographic provinces recognised by Bennett & Pope (1953) (DiBattista *et al.* 2014). Marine gastropods have shown similar genetic structure corresponding to the Bassian Isthmus (Waters *et al.* 2005), and a variety of marine invertebrate species have shown phylogeographic structure in southeast Australia (Ayre *et al.* 2009).

The lack of phylogeographic structuring in the macroalgae I surveyed does not appear to reflect naturally low polymorphism of the genetic markers scored. A variety of markers have been used to investigate macroalgal phylogeography and population genetic variation, and haplotype diversities differ depending on the type of genetic marker employed. For example, it is common for chloroplast markers to show lower haplotype diversity than mitochondrial markers; e.g., *Gracilaria vermiculophylla* (Ohmi) Papenfuss (Yang *et al.* 2008), *Sargassum hemiphyllum* (Turner) C.Agardh (Cheang *et al.* 2010), *Durvillaea potatorum* (Labillardière) Areschoug (Fraser *et al.* 2010), *Macrocystis pyrifera* (Macaya and Zuccarello 2010b), *Mazzaella laminarioides* (Bory de Saint-Vanicent) Fredericq (Montecinos *et al.* 2012), *Pachymeniopsis lanceolata* (K.Okamura) Y.Yamada ex S.Kawabata, *Sargassum polycystum* C.Agardh (Chan *et al.* 2013) and *Pachymeniopsis gargiuli* S.Y.Kim, A.Manghisi, M.Moribato & S.M.Boo (Kim *et al.* 2014). However, the mitochondrial and chloroplast haplotype diversities reported from these studies, 0.390–0.871 and 0.180–0.732 respectively, are typically greater than those observed herein, particularly for chloroplast DNA. These studies have been conducted over comparable ranges (1900–2700 km) to that herein (1100 km), and even across similar geographic settings (e.g., Japan and adjacent Korean mainland). Therefore, the low variation I observed cannot be explained by inherently low variation of the markers surveyed.

Contrasting *Ecklonia radiata* and *Lessonia corrugata* against *Phyllospora comosa* and *M. pyrifera* highlights how differences in morphology (presence of gas-filled vesicles) may have lead to some species displaying genetic structure and some showing shallow to no variation. The structure for *L. corrugata* for instance is consistent with studies of other *Lessonia*, which infer poor capacity for dispersal and limited gene flow (e.g., Martinez *et al.* 2003; Faugeron *et al.* 2005; Tellier *et al.* 2009; Tellier *et al.* 2011). Morphological adaptations have lead to *Lessonia corrugata* being well adapted to exposed high-energy wave environments, possessing a heavy holdfast and strong stipe potentially resulting in its poor dispersal capabilities (Koehl 1986; Westermeier *et al.* 1994). On the other hand both *M. pyrifera* and *P. comosa* possess gas filled vesicles, which help to promote flotation and long distance-dispersal (Dayton 1985; Martinez *et al.* 2003), structures that *L. corrugata* and *E. radiata* lack.

Historical bottlenecks can explain patterns of shallow genetic variation (Hewitt 1996; Janko *et al.* 2007). While Phillips (2001) ascribes the high macroalgal diversity in temperate Australia to a lack of mass extinction events, the fossil record is inadequate to reveal demographic declines that are of short duration yet still capable of reducing genetic diversity. For example, bottlenecks for macroalgae in other regions have been caused by events operating on decadal time scales, such as a particularly strong El Niño (Martinez *et al.* 2003). Life history mediated bottlenecks, occurring when particular stages of an organism's life history become vulnerable to impacts from abiotic and biotic stressors, can also potentially lead to diminished genetic variation (Lotze *et al.* 2001).

Available data on species thermal tolerance show optimal temperatures for growth and reproduction to occur at 19°C for both *Lessonia nigrescens* Bory de Saint-Vincent (a congener of *L. corrugata*) (Martinez 1999) and *E. radiata* (Kirkman 1984), and 13–17°C for *M. pyrifera* (Liu *et al.* 1984). During periods of interglacial warming (120–132kya), sea surface temperatures in southeast Australia reached 2.4–4.7°C above present day (Cortese *et al.* 2013), temperatures potentially outside the thermal tolerance range of these macroalgae, and temperatures that are expected to reoccur under climate change scenarios (IPCC 2014). Historic periods of warming could have caused species bottlenecks, forcing southward range shifts and overall range reduction in southeast Australia, or a complete loss of populations in this region. Historical bottlenecks resulting from Pleistocene periods of climatic cooling have been invoked for similarly low levels of genetic variation in a tropical macroalga (Hoarau *et al.* 2007b; Chan *et al.* 2013). It is however difficult to imagine the temperate species studied herein suffering bottlenecks during climatic cooling, as ample temperate environments would have existed at lower latitudes in Australia during these periods, and conditions at higher latitudes may have been tolerable; for example, Fraser *et al.* (2009b; 2010) only observed low genetic diversity in *Durvillaea antarctica* (Chamisso) Harriot in areas where it was physically displaced by ice scour, whereas greater genetic diversity, consistent with stable populations, were observed at lower latitudes. Given the latitudinal range of my collection locations, and the lack of genetic variation at lower latitudes, bottlenecks are less likely to be a contributing factor to the observed shallow genetic variation.

A more likely explanation for the low genetic diversity is that these macroalgal species are relatively recent arrivals to cool temperate Australia. Previous genetic analysis of *M. pyrifera* has shown all surveyed Southern Hemisphere populations (Australia, New Zealand, South Africa and South America) form a shallow clade, with much deeper variation among Northern Hemisphere populations, such that the Southern Hemisphere appears to have been colonised 3.00–0.01 Mya from the Northwest Pacific (Coyer *et al.* 2001; Bolton 2010; Macaya and Zuccarello 2010a; Astorga *et al.* 2012). Likewise, it has been hypothesized that Southern Hemisphere *Ecklonia* reflects colonization from the Northern Hemisphere over the last few million years (Shepherd and Edgar 2013), supported by the greater diversity of *Ecklonia* species currently distributed throughout the Northern Hemisphere (Lane *et al.* 2006; Bolton 2010). *Lessonia* also most likely has a Northern Hemisphere ancestry (Bolton 2010), and has since undergone a rapid radiation in the Southern Hemisphere during the last 3.4 Myr, with divergence of *L. corrugata* from its sister lineage, *Lessonia adamsiae* C.H.Hay (Snares Island, New Zealand), ~2 Mya ago (Martin and Zuccarello 2012). The origins of *P. comosa* remain uncertain, as it and all its nearest relatives [e.g., *Seirococcus axillaris* (R.Brown ex Turner) Greville] are endemic to the Southern Hemisphere (Silberfeld *et al.* 2010), and a detailed phylogeny with estimates of divergence time is yet to be reconstructed.

The genetic variation shown between western and eastern sides of Tasmania for *L. corrugata* confirms preliminary suggestions of genetic structure in this species by Martin (2011), and is consistent with that observed for *D. potatorum* (Fraser *et al.* 2009a) and a variety of invertebrates, including species of gastropods and echinoderms (Waters *et al.* 2005; Ayre *et al.* 2009). The historical Bassian Isthmus and influential boundary currents may be responsible for the creation of these genetic discontinuities. As the boundary currents persisted after the inundation of Bass Strait, they may be responsible for recent divergences, or the maintenance of earlier divergences created by other mechanisms (York *et al.* 2008; DiBattista *et al.* 2014). The greater phylogeographic structure in *L. corrugata*, relative to the other three species surveyed herein, is consistent with my predictions of dispersal capability based on the buoyancy of sporophyte life history phases.

Although shallow genetic variation has been reported for other species residing in biodiversity hotspots (e.g., Carranza *et al.* 2004), it is not a common characteristic of these

regions. Most frequently species within these hotspots show deep phylogeographic structuring, owing usually to spatial habitat variability and geographic segregation of populations over millions of years (Cicconardi *et al.* 2010; Cooper *et al.* 2011). When shallow genetic variation has been found, it is suggested to be a result of recent species arrival (Carranza *et al.* 2004). These recent species arrivals can be the result of a species range shift, which are set to become more common with climate change (Hewitt 2004; Jentsch *et al.* 2007). Species within biodiversity hotspots could potentially shift their distributional range away from these areas, leading to a loss of species abundance and diversity within a recognized hotspot (Telwala *et al.* 2013). For species in the southeast of Australia with nowhere further south to retreat from increasing sea surface temperatures (Bates *et al.* 2014b), and perhaps little genetic diversity for adaptation, the chances of extinction and loss of biodiversity could be high (Ayre and Hughes 2004; Bouzat 2010; Maclean and Wilson 2011). This scenario may be further supported by the thermal tolerance ranges for these species occurring at a lower range than the temperatures predicted by climate change scenarios. Such population declines are already visible for *M. pyrifera* along the east coast of Australia (Johnson *et al.* 2011a). These macroalgal declines will have negative implications for the diverse range of marine organisms that rely on these algal beds for habitat, with macroalgal populations found to support a larger variety of associated marine species in comparison to habitats where macroalgae are absent (Murphy *et al.* 2000). The removal of these habitat-forming species has the potential to reduce species abundance in macroalgal-associated communities, contributing to a loss of ecosystem diversity as a whole (Bodkin 1988; Ling 2008). Through understanding the processes that influence the diversity of foundation species like macroalgae, we subsequently gain insights into the processes that additionally influence the diversity of associated marine communities and ecosystem biodiversity.

Acknowledgements

This research was funded by grants from the Australian Research Council Linkage Grant LP100200122 (awarded to GE), the Holsworth Wildlife Research Endowment and the University of Tasmania. Authors would like to thank Liz Oh, Rick Stewart-Smith, Mailie Gall, Bryan Woods, Steffan Howe, Dave Miller, Alecia Bellgrove, Peter Unmack, Adam Smolenski and Nick Beeton for help with sample collections and statistical analyses.

Chapter 6

General discussion

This thesis assessed general trends in macroalgal dispersal capabilities and investigated how historical and contemporary processes have influenced the genetic structure of key macroalgal species in southeast Australia. Ultimately, the aim of this work is to inform our understanding of past and present connectivity between populations, such that future conservation measures, such as MPAs, may best account for, and maintain natural levels of connectivity. To accomplish these goals I first undertook a global meta-analysis to assess the general dispersal capabilities of macroalgae. Utilising genetic tools I then assessed the relative influence of contemporary habitat and environmental processes on dispersal and genetic structure in *Lessonia corrugata* Lucas, a common Laminarian macroalga, in southeast Tasmania. This is an endemic species, restricted to Tasmania with assumed limited dispersal capability based on life history characteristics. Hence, it is an ideal model species for conservation management under scenarios such as climate change.

Finally, to determine whether genetic structure of *L. corrugata* could also be related to historical processes, and if it was typical of other common algal species, I undertook a phylogeographic analysis of *L. corrugata* and three other key habitat forming macroalgal species inhabiting the southeast Australian coastline, *Ecklonia radiata* (C.Agardh) J.Agardh, *Phyllospora comosa* (Labillardière) C.Agardh and *Macrocystis pyrifera* (L.). Overall, this thesis provides an overview of the role geographic distance plays in influencing macroalgal dispersal, connectivity and the presence of isolation by distance (IBD) relationships. Additionally, it reveals phylogeographic structure in key southeast Australian macroalgal species, and highlights the influence of historical processes, habitat and environmental variables on population genetic structure. Furthermore, the culmination of knowledge gained through the studies within this thesis provides essential information for the planning of marine reserves, and other conservation activities that may best represent population genetic structure and protect marine species into the future.

6.1 Influence of distance on dispersal

Species dispersal capabilities largely dictate the degree of connectivity between populations. Marine species capable of long distance dispersal often exhibit great connectivity across large distances, allowing the exchange of genes between distant populations (Kinlan and Gaines 2003; Palumbi 2003). In terms of population persistence, species with the ability to disperse across large geographic ranges are more likely to successfully re-establish populations adversely affected by environmental or anthropogenic disturbances, or colonise new environments situated away from these disturbances (Stachowicz *et al.* 2002; Willis *et al.* 2010; Simpson *et al.* 2014). Understanding species dispersal capabilities is a crucial first step in conservation strategies, from designing marine reserves through to adaptive management via translocations, which afford marine populations protection at adequate geographic scales and across suitable habitat types (Roberts *et al.* 2003; Shanks *et al.* 2003; Almany *et al.* 2009).

In a future of increasing anthropogenic disturbances and habitat fragmentation, marine reverses will become crucial to the long-term persistence of macroalgal populations. Increasing geographic distance between protected populations may restrict macroalgal dispersal and limit genetic connectivity between protected areas, as demonstrated by the trend of IBD across multiple species with varying life histories (Chapter 2). A geographic spacing of 50–100 km between macroalgal populations will generally facilitate dispersal of one migrant per generation (F_{ST} = 0.2), maintaining a level of gene flow such that populations do not diverge genetically (Slatkin 1987; Wang 2004), hence if MPAs or other conservation tools are to take macroalgal dispersal into account, spacing at such a scale may be the minimum to effectively maintain connectivity in the absence of other measures. Similar distances have also been suggested in the design of marine reserves for other taxa such as corals (Almany *et al.* 2009) and fishes (Roberts *et al.* 2001). In addition to reserve spacing, Moffitt *et al*. (2011) demonstrated that the size of each reserve would also influence the effectiveness of Marine Protected Areas (MPAs). A network of many smaller reserves may be more suitable than fewer large reserves, as a wider variety of habitats can be protected and the risks associated with anthropogenic and environmental disturbances

can be lessoned over the reserve network (Roberts *et al.* 2003). However, others have found that larger reserves have a greater capacity to support higher species numbers and ecosystem biodiversity (e.g., Edgar and Barrett 1999; Claudet *et al.* 2008). Although this thesis focused on the spacing of MPAs, rather than their size, future studies could additionally incorporate data in relation to size of protected areas in an effort to better understand optimal MPA design from a population genetics perspective.

The growing body of research that now exists on intraspecific genetic structure in marine species has reduced the need for researchers and managers to undertake their own genetic surveys in order to gain a basic understanding of species dispersal capabilities. Quantitative reviews (such as those in Chapter 2), utilising empirical data that exists within the literature, can answer important fundamental questions about scales of dispersal. If a sufficient number of studies exist within the literature, these reviews can provide appropriate recommendations for the design of conservation reserves, without the need for researchers to resample or repeat analyses. A meta-analysis provides a time and cost effective means to begin planning successful conservation strategies for marine and terrestrial communities for which no existing genetic data exists (e.g., Marczak *et al.* 2010; Vandeperre *et al.* 2011; Durrant *et al.* 2014; Fedrowitz *et al.* 2014). Despite the value of such meta-analyses, there exists much spatial, temporal and species specific variation in patterns of dispersal and gene flow and targeted studies still play an important role in informing conservation strategies where time and money permits.

6.2 Contemporary factors influencing dispersal

Although distance has been the traditional measure of interest when investigating population connectivity and species dispersal capabilities, other factors such as habitat and environmental variables will also have a significant role to play (e.g., Coleman *et al.* 2011a; Coleman 2013; Brennan *et al.* 2014). With climate change and increases in anthropogenic disturbances, landscapes will become more fragmented (Walther *et al.* 2002; Munday *et al.* 2009), and the influence of intervening habitat on population genetic structure will be a primary concern for designing effective networks of MPAs and other

conservation measures. As such, the number of studies incorporating measures of intervening habitat into population genetic assessments (seascape genetics) has increased over the last decade (Manel and Holderegger 2013). Chapter 4 outlines and demonstrates ways to assess the influence of habitat and environmental variables, other than geographic distance, on patterns of population genetic structure.

Intervening habitat was found to significantly influence the dispersal among populations of the habitat forming macroalga *Lessonia corrugata*, as was intervening marine distance. When sand dominated intervening habitats, gene flow was restricted in comparison to when rocky reef was the primary intervening habitat. Additionally, when large proportions of open water (deeper than the euphotic zone) dominated intervening habitats, gene flow was also reduced. Although marine distance influences the genetic structure of *L. corrugata,* consistent with the meta-analysis in Chapter 2, intervening habitat also plays an important role in shaping population genetic structure. However, the generality of these results for macroalgae are difficult to determine because of the difficulties associated with mapping underwater habitats. To date there are only two other seascape genetic studies exploring the role of intervening habitat and hydrodynamic processes in macroalgal population connectivity (*Macrocystis pyrifera* Alberto *et al.* 2011; *Laminaria digitata* Brennan *et al.* 2014). Both studies found particle dispersal models to significantly explain population genetic structure. In the case of Alberto *et al*. (2011), *M. pyrifera* individuals occur at greater depths than *L. corrugata,* which could also mean that *M. pyrifera* responds differently to habitat and hydrodynamics, and could explain why particle dispersal models predicted observed population genetic structure in *M. pyrifera*, but were of lesser importance for *L. corrugata* in my study (Chapter 4) (Kelly and Palumbi 2010; Valero *et al.* 2011).

Despite intervening sandy habitats functioning as a barrier for a variety of rocky reef marine taxa (e.g., Riginos and Nachman 2001; Ayre *et al.* 2009; Coleman and Kelaher 2009; Tellier *et al.* 2011), some species may in fact remain substantially connected across putative barriers. One such example of this can be found in the coral reef clown fish *Amphiprion omanensis*. Genetic connectivity was found between populations of *A.*

omanensis, despite the fact they were separated by > 400 km of intervening sandy habitat (Simpson *et al.* 2014). With a pelagic larval stage that can last up to 3 weeks, there is ample opportunity for hydrodynamic forces (e.g., oceanic currents) to influence dispersal of *A. omanensis*. Furthermore, dispersal of *A. omanensis* across large stretches of sand may be promoted by the fact that they have a pre-competency period prior to settlement, with individuals dispersing across these regions until suitable habitats are encountered (Knight-Jones 1951, 1953; Wilson 1953; Toonen and Pawlik 2001).

Numerous marine studies have endeavored to resolve the relationship between population genetic structure and hydrodynamics (Gilg and Hilbish 2003; Mitarai *et al.* 2009; White *et al.* 2010; Coleman *et al.* 2011b; Coleman *et al.* 2013). In order for these relationships to be investigated, hydrodynamic particle dispersal models must exist that appropriately match the dispersal capabilities of the species under investigation. For example, where species are capable of dispersing over large distances (kilometers), particle dispersal models whose resolution captures large scale oceanic processes may be adequate to predict dispersal. However, for species whose range is closer to the coastline these models tend to lose predictability given the complex range of factors influencing dispersal models in shallow waters (e.g., tidal fluxes, waves, sediment transport and turbulence), and are rarely appropriate for predicting dispersal in subtidal or intertidal species (Alberto *et al.* 2011). Despite the problems associated with predicting dispersal in shallow marine regions, recent advancements have enabled the development of fine scale particle dispersal models (e.g., Condie *et al.* 2005; http://www.csiro.au/connie2/; Muhlin *et al.* 2008). This has allowed researchers the opportunity to include such models in seascape genetic analyses, to gain an understanding of the relationship between hydrodynamics and population genetic structure (Gallego *et al.* 2007; Ierodiaconou *et al.* 2007; Wright and Heyman 2008; Coscia *et al.* 2013).

6.3 Historical processes shaping genetic structure

Caution should be taken when making inferences from seascape genetic analyses. In instances where genetic breaks are found, it may be misleading to conclude that

contemporary processes are the primary factor influencing observed population genetic structure, when in fact observed genetic breaks could be the result of historical processes restricting dispersal. Phylogeographic analyses can reveal underlying historical processes that have influenced instraspecific genetic structure, as well as identify regions that function as dispersal barriers (e.g., Ayre *et al.* 2009; DiBattista *et al.* 2014). Combining contemporary and historical genetic assessments allows for a thorough understanding of the processes that shape contemporary population structure (e.g., Weese *et al.* 2012).

Phylogeographic results from Chapter 5 indicated that Australia's key habitat forming macroalgae might be recent arrivals to southeast Australia (< 3 Mya), given the observed shallow phylogeographic structuring. This is consistent with findings from others suggesting a southward range expansion from the Northern Hemisphere in several lineages (Coyer *et al.* 2001; Macaya and Zuccarello 2010b; Shepherd and Edgar 2013). Despite the shallow phylogeographic structuring, potential influences of historical processes were still evident. East-west differentiation observed in *Ecklonia radiata* corresponds to a known biogeographic dispersal barrier, the land bridge (Bassian Isthimus) that once connected Tasmania to mainland Australia, which is an influential factor in the genetic structuring of a variety of other marine taxa (Waters *et al.* 2005; Ayre *et al.* 2009). Although this land bridge may once have been the primary factor responsible for restricting dispersal, the persistence of this genetic discontinuity could be the result of contemporary oceanic boundary currents maintaining population isolation (Bennett and Pope 1953; O'Hara and Poore 2000; Coleman *et al.* 2011b). In such instances it may also be important to assess the taxonomy of genetically isolated forms, as they may in fact correspond to cryptic species (Fraser *et al.* 2009a; Gonzalez *et al.* 2012).

The shallow phylogeographic structure found in Chapter 5 raises concerns for the future of these macroalgal species under fluctuating climatic conditions. With low genetic diversity these populations may not possess genotypes that allow rapid adaptation to climate change. These macroalgal populations, and the associated marine communities they support, may therefore be at risk of extinction with climate change (Johnson *et al.* 2011a; Maclean and Wilson 2011). Due to the absence of any major past extinction events for temperate

Australian marine macroalgae (Edyvane 2003), we are ill equipped to determine their potential response to climate change as we have no historical events to derive expectations. Furthermore, the magnitude of anticipated marine climate change in southeast Australia is higher than anywhere else in the world (Hobday and Pecl 2014).

Patterns of macroalgal population recovery after historical catastrophic climatic events such as El Niño's (Dayton and Tegner 1984; Glynn 1988) and recent events such as marine heatwaves (Wernberg *et al.* 2012 ; Smale and Wernberg 2013) may help inform the likely responses of macroalgae to future climatic changes. Anthropogenic disturbances will also play a key role in macroalgal persistence and population recovery following climatic fluctuations. Given that mitigating climatic changes are largely beyond the control of managers, decreasing anthropogenic stressors in marine environments with conservation measures such as Marine Protected Areas, may help increase the resilience and persistence of macroalgal populations into the future.

6.4 Implications for conservation management

Through undertaking a quantitative literature review and comprehensive genetic analyses, this thesis has demonstrated crucial steps in the design of appropriately constructed MPAs, and other conservation measures such as assisted translocations. Firstly, it is important to understand the geographic dispersal capabilities of key species under protection. Knowing how far apart populations can be located whilst still maintaining gene flow will help determine the spacing in networks of marine reserves (Palumbi 2003; Shanks *et al.* 2003; Durrant *et al.* 2014). Secondly, through seascape genetic analysis, conservation managers can establish the particular types of intervening habitat that would be most advantageous to include in protected regions that facilitate species dispersal, as well as habitat types that represent barriers to dispersal. This information will also be useful for informing whether assisted translocation may be required to cross such dispersal barriers for adaptation to climate change or reestablishment of lost populations. Finally, through phylogeographic analysis, researchers can ascertain whether the results from seascape genetic analyses are the result of contemporary or historical forces influencing species connectivity, and can

highlight biogeographic barriers that may also need to be considered in reserve design (Commonwealth of Australia 2005).

Unfortunately marine reserves have not always been placed in areas that adequately protect species or facilitate population connectivity (Edgar *et al.* 2014), with socio-economic and political factors frequently influencing reserve locations rather than good network design. Declines in key habitats and species including macroalgae are common (e.g., Coleman *et al.* 2008; Connell *et al.* 2008) despite the presence of existing networks of MPAs. To mitigate habitat fragmentation or population loss, translocations can be undertaken in an effort to re-introduce individuals back into areas they once occupied and rehabilitate and maintain the genetic fitness of communities adversely impacted by environmental or anthropogenic stressors. Translocations are frequently proposed and undertaken in terrestrial ecosystems, with strategies developed to overcome genetic risks associated with translocations such as outbreeding depression (Weeks *et al.* 2011). However, in the marine realm such restoration strategies are yet to be fully embraced (although see examples by Sheridan 2004; Lintermans 2013; Campbell *et al.* 2014). Results found in my thesis would be useful for projects undertaking macroalgal translocations as they highlight factors that facilitate and hinder dispersal and characterise natural patterns of genetic diversity and gene flow, both important considerations when planning translocations.

6.5 Future directions

With advances in genetic sequencing technologies (Elliott *et al.* 2014; Van Dijk *et al.* 2014), coupled with the advances in marine habitat mapping and particle dispersal models (Ierodiaconou *et al.* 2007; Wright and Heyman 2008; Edgar and Stuart-Smith 2014), seascape genetic analyses will become more refined. This will result in a deeper understanding about the processes that shape connectivity among marine populations, and allow for more substantial and appropriate conservation plans and rehabilitation programs for species under threat from environmental change and anthropogenic disturbance. Seascape genetic studies would be advanced and refined to maximise habitat and environmental explanatory variables and minimise confounding factors. For example, a

priori site selection could be based on observed correlation coefficients among predictor variables prior to sample collection, allowing specific hypotheses to be tested. In particular, the mutually exclusive nature of marine habitat variables (reef, sand, deep water) needs to be considered during analyses. Hierarchical sampling designs with independently replicable habitat types can help tease apart the general importance of these factors to gene flow.

In addition to habitat heterogeneity (presence of sand, reef and open water), estuaries and embayments can also influence genetic differentiation in species whose distributional ranges span these areas (e.g., Watts and Johnson 2004; Coleman 2013). Depending on the amount of freshwater input upstream, temperature and salinity within an estuary can differ considerably to bordering marine waters (Herzfeld *et al.* 2010), both of which are known to influence larval development and growth (e.g., Byrne *et al.* 2009; Deschaseaux *et al.* 2011). In southern Tasmania the Huon Estuary contains a large amount of freshwater due to its connection with the Huon River upstream, creating a stratified salinity gradient around the point of outfall into the marine waters of the D'Entrecasteaux Channel (Herzfeld *et al.* 2010). This southern Tasmanian coastline provides an ideal location for seascape genetic studies. With the incorporation of two prominent bays to the south of the estuary (Dover and Southport) any influence of open water influencing dispersal could be accounted for, and influences of the estuary on dispersal could be realised. The ability of such factors to influence dispersal and gene flow was demonstrated in Chapter 5 with *Lessonia corrugata* displaying phylogeographic differentiation corresponding to this region (between sites 6 and 11), highlighting the presence of influential dispersal barriers that would benefit from further investigation.

If cross-species amplification of microsatellite genetic markers developed in Chapter 3 was successful, they may prove useful in defining population genetic structure in other *Lessonia* species throughout the Southern Hemisphere. *Lessonia* species are widely known for restricted dispersal capabilities and it would be advantageous to know whether all *Lessonia* species are similarly influenced by habitat and hydrodynamics, or whether this relationship is specific to a species and region. Furthermore, seascape genetic analysis of

other key macroalgal species within the geographic region sampled in Chapter 4 (Derwent Estuary) could further confirm whether the influences of habitat on genetic structure are conserved or idiosyncratic among species. Of particular interest would be macroalgal species that differ morphologically to *L. corrugata*. For macroalgae possessing flotation structures, particle dispersal models might be expected to better predict gene flow. If morphology was found to influence dispersal, it may be possible to identify morphological traits that increase a species ability to traverse contemporary dispersal barriers, ultimately influencing the location of marine reserves that aim to protect these macroalgal communities. Additionally, to further understand relationships between life history and population genetic structure, representative species of varying life histories could be targeted for future research. For example, alternation of generations reproduction was largely represented in Chapter 2 and therefore it may be beneficial to focus future sampling efforts on species displaying differing life histories.

6.6 Conclusions

This thesis has demonstrated the wealth of fundamental information that can be gained about species population structure and dispersal capabilities through utilising results from available literature. This not only saves time, but also saves project funding for more complex analyses that aim to extend our knowledge of population structure and species level dispersal. As the field of seascape genetics grows it will be possible for conservation managers to first undertake reviews such as meta-analyses to determine the general influence of a variety of factors on species dispersal, leading to well constructed and successful conservation reserves. Ultimately, this will also aid in adaptive management strategies that will be required as habitat and environmental variables begin to fluctuate with climate change. This thesis has not only established how contemporary processes, such as environment and habitat, can influence population genetic structure but has also demonstrated the importance of considering historical processes in explaining biogeographical patterns. Species life history also has the capacity to influence dispersal, and can play an important role in explaining characteristics such as endemism (e.g., *Lessonia corrugata*). Ultimately more empirical studies of this nature are needed to better

understand life history relationships with population genetic structure to be able to predict species in need of conservation measures in a time of unparalleled changing environmental conditions

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Supplementary material

Table S1 (Chapter 2) – Summary of studies used in the meta-analysis

Table S2 (Chapter 2) – Summary of studies used in the meta-analysis with corresponding data.

Table S3 (Chapter 4) – Coordinates for sampling locations

Table S4 (Chapter 4) – Probabilities of each location acting as a source of propagules for other locations

Figure S1 (Chapter 4) – Results from STRUCTURE analysis ($K = 3$)

Figure S2 (Chapter 4) – Plot of Delta K and mean LnP(K)

Figure S3 (Chapter 4) – Aus-Connie predicted dispersal probability of propagules

Table S5 (Chapter 5) – Table of sample locations with site abbreviation codes and corresponding GPS coordinates

Table S6 (Chapter 5) – GenBank accession numbers for each individual sampled

Figure S4 (Chapter 5) – Results from a Spatial Analysis of Molecular Variance (SAMOVA)

Supplementary material to chapter 2

Table S1: Summary of studies used in the meta-analysis. Isolation by distance correlation coefficients (r), sample size (n), effect size (Z) genetic marker (Marker), algal division/taxa (division), life cycle type (alternating generations, monoecious & dioecious) and macroalgae habitat (Habitat), were all used in the meta-analysis process. The author (Source) and species in each study are also shown.

Source	Species	Habitat	Life cycle type	Division	Marker	*n*	*Z*	*r*
Alberto *et al*. (2010)	*Macrocystis pyrifera*	Subtidal	Alternating	Phaeophyta	Msat	50	0.648	0.570
Alberto *et al*. (2011)	*Macrocystis pyrifera*	Subtidal	Alternating	Phaeophyta	Msat	50	1.116	0.806
Billot *et al*. (2003)	*Laminaria digitata*	Intertidal	Alternating	Phaeophyta	Msat	438	0.187	0.184
Bouza *et al*. (2006)	*Gelidium canariense*	Intertidal	Alternating	Rhodophyta	RAPD	190	0.987	0.756
Coleman & Brawley (2005a)	*Fucus spiralis*	Intertidal	Monoecious	Phaeophyta	Msat	200	0.215	0.212
Coleman & Brawley (2005b)	*Fucus distichus*	Intertidal	Monoecious	Phaeophyta	Msat	336	0.288	0.280
Coleman *et al*. (2011a)	*Hormosira banksii*	Intertidal	Dioecious	Phaeophyta	Msat	704	0.980	0.753
Coleman *et al*. (2009a)	*Ecklonia radiata*	Subtidal	Alternating	Phaeophyta	Msat	32	1.020	0.770
Coleman and Kelaher (2009)	*Phyllospora comosa*	Subtidal	Dioecious	Phaeophyta	Msat	392	0.014	0.014
Coleman *et al*. (2011b)	*Ecklonia radiata*	Subtidal	Alternating	Phaeophyta	Msat	351	1.221	0.840
Coleman *et al*. (2011b)	*Ecklonia radiata*	Subtidal	Alternating	Phaeophyta	Msat	405	0.872	0.703
Coleman *et al*. (2011b)	*Ecklonia radiata*	Subtidal	Alternating	Phaeophyta	Msat	713	0.123	0.122
Couceiro *et al*. (2011)	*Ahnfeltiopsis pusilla*	Intertidal	Alternating	Rhodophyta	AFLP	110	1.472	0.900
Coyer *et al*. (2003)	*Fucus serratus*	Intertidal	Dioecious	Phaeophyta	Msat	1343	0.759	0.640
Engelen *et al*. (2001)	*Sargassum polyceratium*	Intertidal	Dioecious	Phaeophyta	RAPD	188	0.220	0.216
Fraser *et al*. (2010a)	*Durvillaea antarctica*	Intertidal	Dioecious	Phaeophyta	COI/rbcL	164	0.255	0.249

Kusumo *et al*. (2006)	*Postelsia palmaeformis*	Intertidal	Alternating	Phaeophyta	Msat	245	0.671	0.586
Kusumo & Druehl (2000)	*Alaria marginata*	Intertidal	Alternating	Phaeophyta	AFLP	71	0.358	0.343
Maneiro *et al*. (2011)	*Grateloupia lanceola*	Intertidal	Alternating	Rhodophyta	AFLP	225	1.570	0.917
Martinez *et al*. (2003)	*Lessonia nigrescens*	Intertidal	Alternating	Phaeophyta	RAPD	121	0.631	0.559
Muhlin and Brawley (2009)	*Fucus vesiculosus*	Intertidal	Dioecious	Phaeophyta	Msat	241	0.969	0.748
Tatarenkov *et al*. (2007)	*Fucus vesiculosus*	Intertidal	Dioecious	Phaeophyta	Msat	1200	0.845	0.688
Van der Strate et al. (2003)	*Cladophoropsis membranacea*	Intertidal	Alternating	Chlorophyta	Msat	117	0.409	0.387
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	Intertidal	Alternating	Chlorophyta	Msat	85	0.693	0.600
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	Intertidal	Alternating	Chlorophyta	Msat	65	0.576	0.520
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	Intertidal	Alternating	Chlorophyta	Msat	273	0.005	0.005
Wright *et al*. (2000)	*Delisea pulchra*	Subtidal	Alternating	Rhodophyta	RAPD	89	0.127	0.126
Wright *et al*. (2000)	*Delisea pulchra*	Subtidal	Alternating	Rhodophyta	RAPD	60	0.077	0.077
Zhao *et al*. (2008)	*Sargassum muticum*	Intertidal	Monoecious	Phaeophyta	RAPD	84	0.975	0.751
Zhao *et al*. (2007)	*Sargassum thunbergii*	Intertidal	Monoecious	Phaeophyta	RAPD	84	0.911	0.722

Table S1 literature cited

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Table S2: Summary of studies used in the correlation showing: Author (Source), species and same size (n), F_{ST} values, geographic scale and genetic distance (F_{ST} / (1-F_{ST})).

Source	species	*n* (total)	F_{ST}	scale (km)	F_{ST} / (1-F_{ST})
Alberto *et al*. (2010)	*Macrocystis pyrifera*	50	0.021	75.000	0.021
Alberto *et al*. (2011)	*Macrocystis pyrifera*	50	0.021	70.000	0.021
Andreakis *et al*. (2009)	*Asparagopsis taxiformis*	319	0.545	13045.600	1.198
Andreakis *et al*. (2009)	*Asparagopsis taxiformis*	260	0.159	1039.000	0.189
Benzie *et al*. (1997)	*Caulerpa cupressoides*	28	0.912	12.500	10.364
Benzie *et al*. (1997)	*Cecropia peltata*	22	0.000	25.000	0.000
Benzie *et al*. (1997)	*Caulerpa racemosa*.var. *laetevirens*	80	0.266	10.000	0.362
Benzie *et al*. (1997)	*Caulerpa racemosa* var. *racemosa*	59	0.886	60.000	7.772
Benzie *et al*. (1997)	*Caulerpa.serrulata*	44	0.635	60.000	1.740
Benzie *et al*. (1997)	*Caulerpa taxifolia*	110	0.418	70.000	0.718
Billot *et al*. (2003)	*Laminaria digitata*	438	0.068	1000.000	0.073
Billot *et al*. (2003)	*Laminaria digitata*	438	0.042	100.000	0.044
Billot *et al*. (2003)	*Laminaria digitata*	438	0.045	50.000	0.047
Billot *et al*. (2003)	*Laminaria digitata*	438	0.009	2.000	0.009
Bouza *et al*. (2006)	*Gelidium canariense*	190	0.311	230.000	0.451
Bouza *et al*. (2006)	*Gelidium canariense*	148	0.120	75.000	0.136

Coleman & Brawley (2005b)	*Fucus distichus*	336	0.146	80.000	0.171
Coleman & Brawley (2005b)	*Fucus distichus*	336	0.095	6.000	0.105
Coleman & Brawley (2005b)	*Fucus distichus*	336	0.237	0.030	0.311
Coleman & Brawley (2005a)	*Fucus spiralis*	200	0.006	80.000	0.006
Coleman & Brawley (2005a)	*Fucus spiralis*	200	0.039	6.000	0.041
Coleman and Kelaher (2009)	*Phyllospora comosa*	392	0.016	437.600	0.016
Coleman and Kelaher (2009)	*Phyllospora comosa*	392	0.039	203.200	0.041
Coleman and Kelaher (2009)	*Phyllospora comosa*	392	0.048	9.000	0.050
Coleman *et al*. (2009a)	*Ecklonia radiata*	32	0.211	700.000	0.267
Coleman *et al*. (2009a)	*Ecklonia radiata*	32	0.042	45.000	0.044
Coleman *et al*. (2011b)	*Ecklonia radiata*	1469	0.048	5.500	0.050
Coleman *et al*. (2011b)	*Ecklonia radiata*	351	0.211	711.300	0.267
Coleman *et al*. (2011b)	*Ecklonia radiata*	405	0.110	757.600	0.124
Coleman *et al*. (2011b)	*Ecklonia radiata*	713	0.046	816.700	0.048
Coleman *et al*. (2011a)	*Hormosira banksii*	704	0.270	740.000	0.370
Coleman *et al*. (2011a)	*Phyllospora comosa*	480	0.140	150.000	0.163
Coleman *et al*. (2011a)	*Ecklonia radiata*	800	0.049	740.000	0.052
Coyer *et al*. (2003)	*Fucus serratus*	1343	0.170	933.000	0.205
Coyer *et al*. (2006)	*Fucus serratus*	1133	0.340	1661.000	0.516

Coyer *et al*. (2008)	*Fucus serratus*	64	0.017	1.000	0.017
Engel *et al*. (2004)	*Gracilaria gracilis*	296	0.005	0.525	0.005
Engel *et al*. (2004)	*Gracilaria gracilis*	296	0.012	5.000	0.012
Engel *et al*. (2004)	*Gracilaria gracilis*	280	0.020	0.525	0.020
Engel *et al*. (2004)	*Gracilaria gracilis*	280	0.039	5.000	0.041
Engelen *et al*. (2001)	*Sargassum polyceratium*	188	0.283	25.000	0.395
Faugeron *et al*. (2004)	*Gigartina skottsbergii*	78	0.354	55.000	0.548
Faugeron *et al*. (2004)	*Gigartina skottsbergii*	70	0.145	70.000	0.170
Faugeron *et al*. (2004)	*Gigartina skottsbergii*	248	0.488	1000.000	0.953
Faugeron *et al*. (2001)	*Mazzaella laminarioides*	288	0.069	5.000	0.074
Faugeron *et al*. (2001)	*Mazzaella laminarioides*	288	0.011	0.030	0.011
Faugeron *et al*. (2001)	*Mazzaella laminarioides*	288	0.034	0.005	0.035
Faugeron *et al*. (2001)	*Mazzaella laminarioides*	288	0.265	60.000	0.360
Faugeron *et al*. (2005)	*Lessonia nigrescens*	106	0.167	40.000	0.200
Grulois *et al*. (2011)	*Undaria pinnatifida*	955	0.099	19.300	0.110
Guillemin *et al*. (2008)	*Gracilaria chilensis*	410	0.380	460.000	0.613
Johansson *et al*. (2003)	*Cladophora rupestris*	328	0.086	623.800	0.094
Johansson *et al*. (2003)	*Cladophora rupestris*	328	0.348	874.400	0.535
Krueger-Hadfield *et al*. (2011)	*Chondrus crispus*	450	0.028	0.050	0.028

Krueger-Hadfield *et al*. (2011)	*Chondrus crispus*	450	0.201	500.000	0.252
Kusomo *et al*. (2006)	*Postelsia palmaeformis*	245	0.470	11.000	0.887
Kusomo *et al*. (2006)	*Postelsia palmaeformis*	245	0.099	0.033	0.110
Kusumo & Druehl (2000)	*Alaria marginata*	71	0.080	6.500	0.087
Kusumo & Druehl (2000)	*Alaria marginata*	71	0.402	0.005	0.671
Leskinen *et al*. (2004)	*Ulva intestinalis*	106	0.053	2000.000	0.055
Lu & Williams (1994)	*Halidrys dioica*	132	0.040	0.005	0.041
Lu & Williams (1994)	*Halidrys dioica*	288	0.018	4.000	0.018
Lu & Williams (1994)	*Halidrys dioica*	360	0.194	90.000	0.241
Maneiro *et al*. (2011)	*Grateloupia lanceola*	225	0.163	1000.000	0.195
Muhlin and Brawley (2009)	*Fucus vesiculosus*	241	0.552	1800.000	1.232
Muhlin and Brawley (2009)	*Fucus vesiculosus*	346	0.126	440.000	0.144
Muhlin *et al*. (2008)	*Fucus vesiculosus*	320	0.022	500.000	0.022
Muhlin *et al*. (2008)	*Fucus vesiculosus*	320	0.038	9.000	0.040
O'Doherty and Sherwood (2007)	*Acanthophora spicifera*	32	0.609	379.400	1.558
Pearson & Murray (1997)	*Lithothrix aspergillum*	215	0.030	5.500	0.031
Pearson & Murray (1997)	*Lithothrix aspergillum*	275	0.398	70.000	0.661
Pearson & Murray (1997)	*Lithothrix aspergillum*	350	0.618	760.000	1.618
Perrin *et al*. (2007)	*Fucus vesiculosus*	168	0.520	1875.000	1.083

Perrin *et al*. (2007)	*Fucus spiralis*	163	0.300	1875.000	0.429
Sosa and Garcia Reina (1992)	*Gelidium arbuscula*	313	0.334	100.000	0.502
Sosa and Garcia Reina (1992)	*Gelidium arbuscula*	847	0.147	100.000	0.172
Sosa and Garcia Reina (1993)	*Gelidium canariense*	219	0.366	100.000	0.577
Sosa and Garcia Reina (1993)	*Gelidium canariense*	557	0.073	100.000	0.079
Sosa *et al*. (1996)	*Gracilaria cervicornis*	100	0.009	20.000	0.009
Sosa *et al*. (1996)	*Gracilaria cervicornis*	276	0.127	43.000	0.145
Sosa *et al*. (1998)	*Gelidium canariense*	557	0.130	100.000	0.149
Sosa *et al*. (1998)	*Gelidium arbuscula*	847	0.280	100.000	0.389
Tatarenkov *et al*. (2007)	*Fucus vesiculosus*	1200	0.120	800.000	0.136
Tellier *et al*. (2011)	*Lessonia nigrescens*	351	0.479	50.000	0.918
Van der Strate *et al*. (2002)	*Cladophoropsis membranacea*	478	0.032	0.020	0.033
Van der Strate *et al*. (2002)	*Cladophoropsis membranacea*	267	0.056	263.000	0.059
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	117	0.271	126.000	0.372
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	85	0.190	96.000	0.235
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	65	0.270	68.000	0.370
Van der Strate *et al*. (2003)	*Cladophoropsis membranacea*	273	0.056	323.000	0.060
Voisen *et al*. (2005)	*Undaria pinnatifida*	524	0.386	2309.900	0.629
Williams & DiFiori (1996)	*Pelvetia fastigiata*	150	0.806	130.000	4.155

Williams & DiFiori (1996)	*Pelvetia fastigiata*	60	0.005	0.640	0.005
Wright *et al*. (2000)	*Delisea pulchra*	89	0.040	0.023	0.042
Wright *et al*. (2000)	*Delisea pulchra*	60	0.128	0.043	0.146
Wright *et al*. (2000)	*Delisea pulchra*	149	0.084	0.050	0.091
Zhao *et al*. (2011)	*Ulva prolifera*	24	0.646	1155.000	1.825
Zhao *et al*. (2007)	*Sargassum thunbergii*	84	0.576	120.000	1.358
Zhao *et al*. (2008)	*Sargassum muticum*	84	0.558	120.000	1.263
Zuccarello *et al*. (2001)	*Caloglossa leprieurii*	331	0.285	1.000	0.399
Zuccarello *et al*. (2001)	*Caloglossa leprieurii*	331	0.349	0.060	0.536

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Supplementary material to chapter 4

Table S3: Sampling locations

Site	Longitude	Latitude
West 1	42°58'29"S	147°20'15"E
West 2	42°59'11"S	147°19'42"E
West 3	43°00'01"S	147°19'41"E
West 4	43°00'28"S	147°19'46"E
West 5	43°01'03"S	147°19'47"E
West 6	43°02'20"S	147°20'16"E
East 1	42°58'43"S	147°23'41"E
East 2	42°59'39"S	147°23'55”E
East 3	42°59'54"S	147°23'52"E
East 4	43°00'30"S	147°23'57"E
East 5	43°02'15"S	147°24'15"E
East 6	43°02’19"S	147°24'30"E
East 7	43°02'46"S	147°24'28"E
South	43°03'57"S	147°21'36"E

Table S4: Probabilities of each location acting as a source of propagules for other locations. The top right section of the matrix displays results for northward dispersal routes and bottom left shows results for southward dispersal routes.

	West 1	West 2	West 3	West 4	West 5	West 6	East 1	East 2	East 3	East 4	East 5	East 6	East 7	South
West 1	-	0.006	0	0	0	0	0	0	0	0	0	0	0	0
West 2	0.164	-	0.002	0	0	0	0	0	0	0	0	0	0	0
West 3	0.091	0.316	-	0.021	0.002	0	0	0	0	0	0	0	0	0
West 4	0.065	0.198	0.524	-	0.053	0	0	0	0	0	0	0	0	0
West 5	0.027	0.086	0.198	0.404	-	0	0	0	0	0	0	0	0	0.006
West 6	0.021	0.071	0.223	0.297	0.358	-	0	0	0	0	0	0	0	0
East 1	0	0	0	0	0	0	-	0.011	0	0	0	0	0	0
East 2	0	0	0	0	0	0	0.124	-	0.019	0	0	0	0	0
East 3	0	0	0	0	0	0	0.011	0.011	-	0	0	0	0	0
East 4	0	0	0	0	0	0	0.463	0.011	0.011	-	0	0	0	0
East 5	0	0	0	0	0	0	0.015	0.002	0	0.065	-	0	0	0
East 6	0	0	0	0	0	0	0.013	0.002	0	0.059	0.941	-	0.002	0
East 7	0	0	0	0	0	0	0.017	0.002	0	0.067	0.869	0.019	-	0
South	0.034	0.053	0.120	0.084	0.069	0.074	0	0	0	0	0.004	0	0	-

*Note: In cases where dispersal was bidirectional, the largest probability value was used in multivariate analyses.

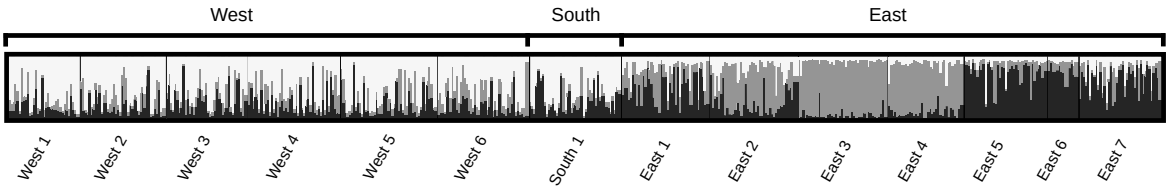

Figure S1: Results from STRUCTURE analysis, showing $K = 3$ clusters. Each bar represents an individual within a location, with each colour shade representing the coancestry coefficient of that individual belonging to a particular cluster.

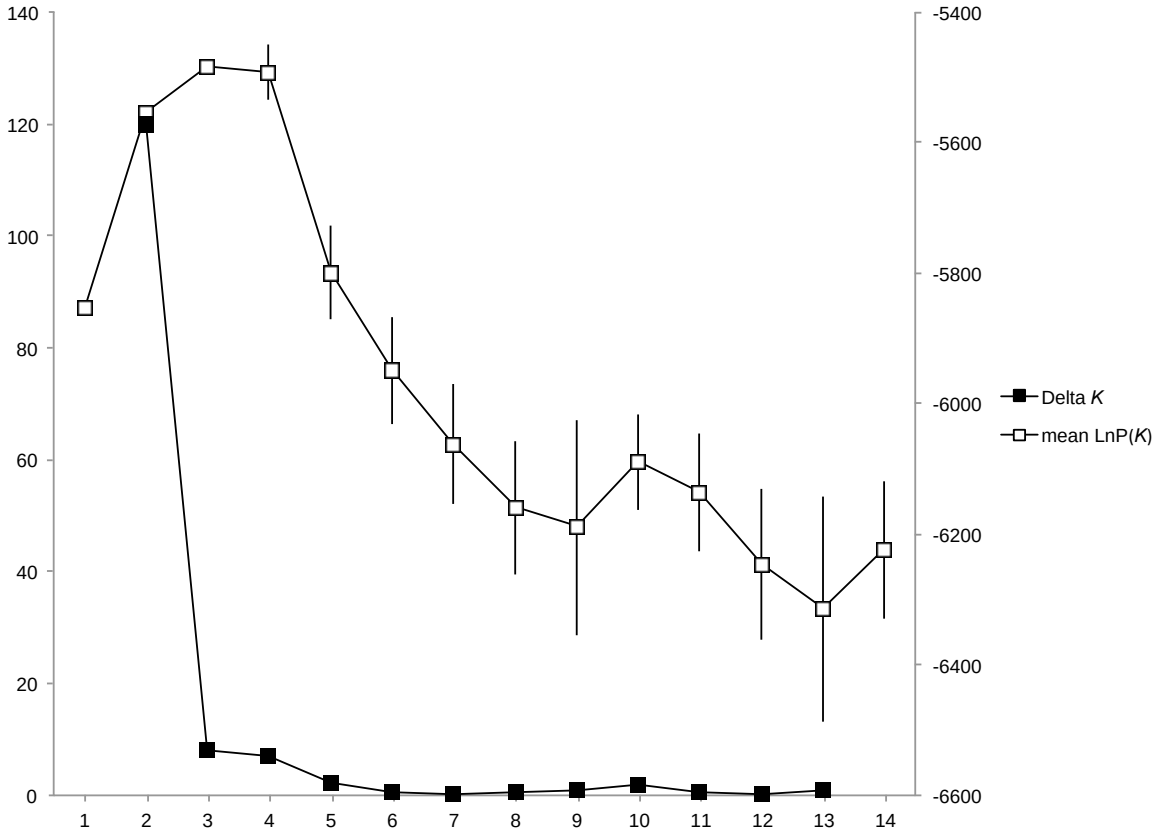

Figure S2: Plot of Delta *K* and mean LnP(*K*) (±SD, represented by error bars) per cluster (*K*), based on 20 replicates of *K* during STRUCTURE analysis.

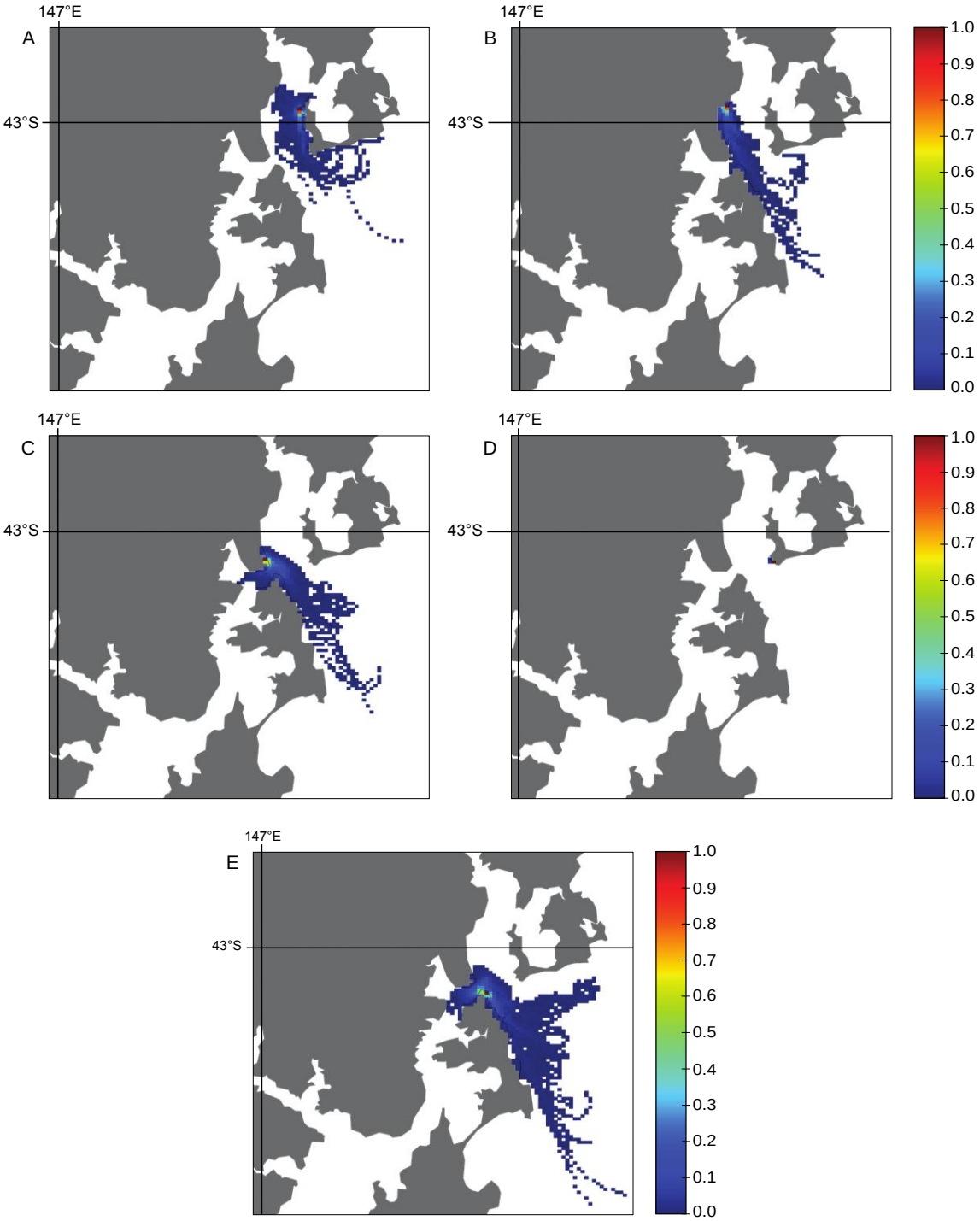

Figure S3: Aus-Connie predicted dispersal probability of propagules after a 2 day dispersal period: A) Release site at East 1, B) Release site at West 1, C) Release site at West 6, D) Release site at East 7 and E) Release site at the most southern site (South).

Supplementary material to chapter 5

Table S5: Table of sample locations with site abbreviation codes and corresponding GPS coordinates. Tas= Tasmania, NSW= New South Wales, SA=South Australia and VIC=Victoria, N_{cp} and N_{mt}= total number of individuals sequenced per site for chloroplast (N_{cp}) and mitochondrial (N_{mt}) genetic markers.

Species	Site	Site number	Code	MPA	Location	N_{cp}	N_{mt}	Lat	Long
Ecklonia radiata	Myponga South	1.1	MSSA	Encounter Bay	SA	3	5	-35.388	138.349
	Snapper North	1.2	SNSA	Encounter Bay	SA	4	3	-35.75	138.055
	Flat Irons	1.3	FISA	Encounter Bay	SA	2	5	-35.618	138.557
	Baudin Rocks	2.1	BRSA	Robe	SA	4	5	-37.085	139.721
	Goat Island	2.2	GISA	Robe	SA	1	3	-37.177	139.735
	Inner saddle	5.1	ISPTD	Port Davey	Tas	3	4	-43.303	145.903
	Farrel Point	5.3	FPPTD	Port Davey	Tas	5	5	-43.34	146.085
	Muttonbird Island	5.5	MIPTD	Port Davey	Tas	4	3	-43.417	145.972
	Drum and Drunkstick	7.1	DDNSW	Jervis Bay	NSW	4	5	-35.048	150.84
	Outer tubes	7.2	OTNSW	Jervis Bay	NSW	5	4	-35.088	150.799
	Callala Reef	7.3	CRNSW	Jervis Bay	NSW	4	4	-35.012	150.717
	Hogan island	8.1	HIK	Kent group	Tas	0	4	-39.219	146.992
	Erith Island	8.2	EIK	Kent group	Tas	3	4	-39.444	147.285
	Binalong Bay	9.1	BB	Bay of Fires*	Tas	4	5	-41.246	148.304
	Skeleton Bay	9.2	SB	Bay of Fires*	Tas	2	0	-41.254	148.317
	Oakhampton	10.1	OT	Triabunna	Tas	5	3	-42.524	147.969
	Point Holme	10.2	PHT	Triabunna	Tas	2	2	-42.553	147.948
	Green Bluff	10.5	GBMI	Maria Island	Tas	2	3	-42.72	148.011

	Blackmans Bay	11.1	BBT	Tinderbox	Tas	5	5	-43.012	147.331
	Lucas point	11.2	LPT	Tinderbox	Tas	4	4	-43.038	147.339
	Dennes Point	11.3	DPT	Tinderbox	Tas	1	4	-43.063	147.357
Macrocystis pyrifera	Baudin Rocks	2.1	BRSA	Robe	SA	4	4	-37.085	139.721
	Goat Island	2.2	GISA	Robe	SA	4	4	-37.177	139.735
	Inner Saddle	5.1	ISPTD	Port Davey	Tas	4	2	-43.303	145.903
	Whalers Beach	5.2	WBPTD	Port Davey	Tas	5	2	-43.291	145.923
	Muttonbird Island	5.5	MIPTD	Port Davey	Tas	5	4	-43.417	145.972
	Huon Island	6.1	HIC	Channel	Tas	5	4	-43.294	147.142
	Blackmans Bay	11.1	BBT	Tinderbox	Tas	5	3	-43.012	147.331
	Lucas Point	11.2	LPT	Tinderbox	Tas	4	3	-43.038	147.339
	Warrnambool	3	WBVIC	Merri	Vic	5	2	-38.402	142.474
Phyllospora comosa	Goat Island	2.2	GISA	Robe	SA	5	5	-37.177	139.735
	Merlin inner	4.1	MIVIC	Port Phillip Heads	Vic	5	5	-38.289	144.619
	Nepean Inner	4.2	NIVIC	Port Phillip Heads	Vic	5	5	-38.306	144.658
	Inner saddle	5.1	ISPTD	Port Davey	Tas	5	4	-43.303	145.903
	Whalers Beach	5.2	WBPTD	Port Davey	Tas	5	5	-43.291	145.923
	Muttonbird Island	5.5	MIPTD	Port Davey	Tas	5	5	-43.417	145.972
	Huon Island	6.1	HIC	Channel	Tas	5	5	-43.294	147.142
	Nine Pin Point	6.2	NPC	Channel	Tas	5	4	-43.285	147.167
	Arch Rock	6.3	ARC	Channel	Tas	5	4	-43.288	147.179
	Callala Reef	7.3	CRNSW	Jervis Bay	NSW	5	5	-35.012	150.717

	Plantation point	7.4	PPNSW	Jervis Bay	NSW	5	4	-35.07	150.698
	Captains Point	7.5	CPNSW	Jervis Bay	NSW	5	5	-35.121	150.708
	Hogan island	8.1	HIK	Kent group	Tas	5	4	-39.219	146.992
	Erith Island	8.2	EIK	Kent group	Tas	5	4	-39.444	147.285
	Squally cove	8.3	SCK	Kent group	Tas	5	5	-39.493	147.342
	Binalong Bay	9.1	BB	Bay of Fires*	Tas	5	5	-41.246	148.304
	Skeleton Bay	9.2	SB	Bay of Fires*	Tas	5	5	-41.254	148.317
	Oakhampton	10.1	OT	Triabnunna	Tas	5	5	-42.524	147.969
	Point Holme	10.2	PHT	Triabunna	Tas	4	5	-42.553	147.948
	Green Bluff	10.5	GBMI	Maria Island	Tas	5	5	-42.72	148.011
Lessonia corrugata	Inner Saddle	5.1	ISPTD	Port Davey	Tas	4	5	-43.312	145.897
	Normon Cove	5.4	NCPTD	Port Davey	Tas	3	5	-43.369	145.933
	Muttonbird Island	5.5	MIPTD	Port Davey	Tas	5	5	-43.417	145.972
	Huon Island	6.1	HIC	Channel	Tas	5	5	-43.294	147.142
	Point Holme	10.2	PHT	Triabunna	Tas	5	4	-42.562	148.067
	Spring Beach	10.3	SBT	Triabunna	Tas	5	4	-42.584	147.916
	Isle de nord	10.4	INMI	Maria Island	Tas	5	5	-42.553	147.948
	Blackmans Bay	11.1	BBT	Tinderbox	Tas	4	1	-43.012	147.331
	Lucas Point	11.2	LPT	Tinderbox	Tas	4	5	-43.038	147.339

Table S6: A list of GenBank accession numbers, for mitochondrial (rbcL) and chloroplast (COI) genetic markers, corresponding to each individual sampled.

Individual	Species	Marker	GenBank accession
1	*Ecklonia radiata*	rbcL	KT158718
2	*Ecklonia radiata*	rbcL	KT158719
3	*Ecklonia radiata*	rbcL	KT158720
4	*Ecklonia radiata*	rbcL	KT158721
5	*Ecklonia radiata*	rbcL	KT158722
6	*Ecklonia radiata*	rbcL	KT158723
7	*Ecklonia radiata*	rbcL	KT158724
8	*Ecklonia radiata*	rbcL	KT158725
9	*Ecklonia radiata*	rbcL	KT158726
10	*Ecklonia radiata*	rbcL	KT158727
11	*Ecklonia radiata*	rbcL	KT158728
12	*Ecklonia radiata*	rbcL	KT158729
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14	*Ecklonia radiata*	rbcL	KT158731
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18	*Ecklonia radiata*	rbcL	KT158735
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45	*Ecklonia radiata*	rbcL	KT158762
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10	*Lessonia corrugata*	COI	KT158914
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12	*Lessonia corrugata*	COI	KT158916
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14	*Lessonia corrugata*	COI	KT158918
15	*Lessonia corrugata*	COI	KT158919
16	*Lessonia corrugata*	COI	KT158920
17	*Lessonia corrugata*	COI	KT158921
18	*Lessonia corrugata*	COI	KT158922
19	*Lessonia corrugata*	COI	KT158923
20	*Lessonia corrugata*	COI	KT158924
21	*Lessonia corrugata*	COI	KT158925
22	*Lessonia corrugata*	COI	KT158926
23	*Lessonia corrugata*	COI	KT158927
24	*Lessonia corrugata*	COI	KT158928
25	*Lessonia corrugata*	COI	KT158929
26	*Lessonia corrugata*	COI	KT158930
27	*Lessonia corrugata*	COI	KT158931
28	*Lessonia corrugata*	COI	KT158932
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31	*Lessonia corrugata*	COI	KT158935
32	*Lessonia corrugata*	COI	KT158936

33	*Lessonia corrugata*	COI	KT158937
34	*Lessonia corrugata*	COI	KT158938
35	*Lessonia corrugata*	COI	KT158939
36	*Lessonia corrugata*	COI	KT158940
37	*Lessonia corrugata*	COI	KT158941
38	*Lessonia corrugata*	COI	KT158942
39	*Lessonia corrugata*	COI	KT158943
1	*Macrocystis pyrifera*	rbcL	KT158944
2	*Macrocystis pyrifera*	rbcL	KT158945
3	*Macrocystis pyrifera*	rbcL	KT158946
4	*Macrocystis pyrifera*	rbcL	KT158947
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6	*Macrocystis pyrifera*	rbcL	KT158949
7	*Macrocystis pyrifera*	rbcL	KT158950
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16	*Macrocystis pyrifera*	rbcL	KT158959
17	*Macrocystis pyrifera*	rbcL	KT158960
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19	*Macrocystis pyrifera*	rbcL	KT158962
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21	*Macrocystis pyrifera*	rbcL	KT158964
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38	*Macrocystis pyrifera*	rbcL	KT158981
39	*Macrocystis pyrifera*	rbcL	KT158982
40	*Macrocystis pyrifera*	rbcL	KT158983
41	*Macrocystis pyrifera*	rbcL	KT158984
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24	*Macrocystis pyrifera*	COI	KT159008
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27	*Macrocystis pyrifera*	COI	KT159011
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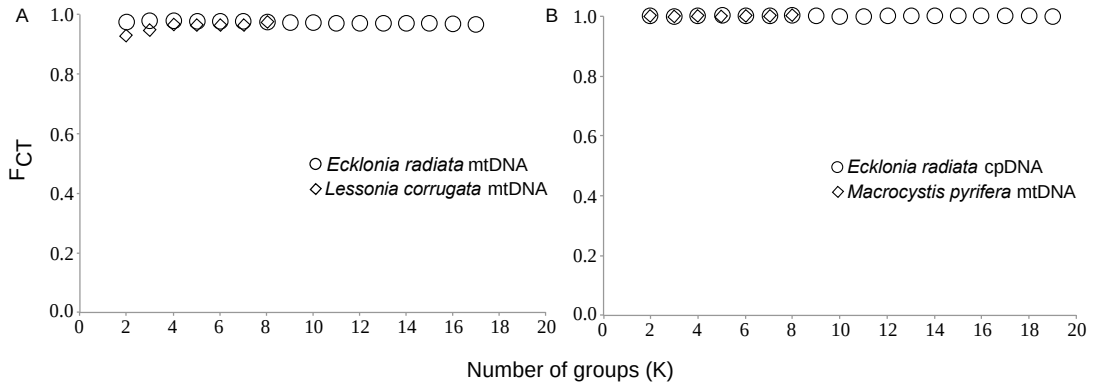

Figure S4: Results from a Spatial Analysis of Molecular Variance (SAMOVA). A) *Ecklonia radiata* mitochondrial marker and *Lessonia corrugata* mitochondrial and B) *Ecklonia radiata* chloroplast marker and *Macrocystis pyrifera* mitochondrial marker. F_{CT}= the proportion of genetic variation among groups. F_{SC} (the proportion of genetic variation among populations within groups) is expected to decline with group increases.